FACTORS AFFECTING SURVIVAL OF ARCTIC-BREEDING DUNLIN

(*CALIDRIS ALPINA ARCTICOLA*) ADULTS AND CHICKS

By

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FACTORS AFFECTING SURVIVAL OF ARCTIC-BREEDING DUNLIN (*CALIDRIS ALPINA ARCTICOLA*) ADULTS AND CHICKS

A

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ABSTRACT

Accurate estimates of, and identifying factors affecting, survival and productivity can provide insight into population trends and help determine what management actions would most benefit a population. Only limited demographic data are available for many arctic-breeding shorebird species. I estimated survival probabilities for arctic-breeding Dunlin (*Calidris alpina arcticola*); for adults between 2003 and 2010, and for chicks in 2008 and 2009. Adult apparent survival probabilities were higher for males (0.60 ± 0.04) than females (0.41 ± 0.05), were higher for individuals initiating nests earlier in the season, and yearly variation was high. These apparent survival rates appear insufficient to maintain a stable population. Daily survival rates of chicks increased as insect biomass increased across all ages and hatch dates, but the relationship with age and hatch date depended on the values of the other variables. The probability of a chick surviving to 15 days of age showed a strong relationship with hatch date, peaking in early July then declining rapidly. Chick survival was much higher for young from first nests (0.71 ± 0.07) than early (0.23 ± 0.19) or late (0.03 ± 0.61) replacement nests. This suggests replacement nests make a much smaller contribution to annual recruitment than first nests.

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General Introduction

Shorebirds are a diverse taxa that inhabit most regions of the world (Colwell 2010). Many species are highly migratory, traveling hundreds to thousands of kilometers twice a year between the wintering and breeding grounds. While the physical strain the birds endure is a feat in itself (e.g., Gill et al. 2009), like most migratory birds, shorebirds must also adapt to new challenges, including loss of habitat from anthropogenic activities (e.g., Yang et al. 2011) and from climate change (Galbraith et al. 2002). Other challenges to their survival include disease, environmental contamination, disturbance, and changes in predator and prey abundances (Butler et al. 2004). Forty-eight percent of the world's 200 shorebird species are declining (Brown et al. 2001, Thomas et al. 2006, Bart et al. 2007), but how various impacts are contributing to these declines is generally not known (Brown et al. 2001, Butler et al. 2004). We need to determine what demographic parameters are driving population growth rates as well as the relationships of these demographic parameters with different potential impacts to enable effective and efficient conservation efforts that are directed where they will be most beneficial.

Studies have shown that shorebirds are a so-called "bet-hedging" species, characterized by moderate to high adult survival, early maturation, and highly variable reproductive output (Sæther et al. 1996). Previous studies of sandpiper populations have shown that adult survival is the parameter that population growth rate is most sensitive to, meaning that changes in adult survival will result in the greatest changes in the population growth rate (Hitchcock and Gratto-Trevor 1997, Ottvall and Härdling 2005, Koivula et al. 2008, Pakanen et al. 2010). However, changes to juvenile survival (i.e., first year survival; Ottvall and Härdling 2005, Koivula et al. 2008), nest success (Ottvall and Härdling 2005, Koivula et al. 2008), and the rate of immigration (Hitchcock and Gratto-Trevor 1997, Koivula et al. 2008) can also result in non-negligible changes in population growth rate. Although many shorebird species have analogous life history traits which predispose their populations to respond similarly to changes in demographic processes (Sæther et al. 1996, Sæther and Bakke 2000), the threats faced by species on

the breeding, migratory stopover, and non-breeding grounds may differ. Thus, individual studies may be required to understand how potential impacts are affecting demographic rates and the subsequent consequences to population growth.

While estimates of adult survival rates have been determined for many shorebird species, most studies have relied on simple return rates as a measure of survival (Sandercock 2003, Colwell 2010). Because return rates are the probabilities of four factors (true survival, site fidelity, site propensity, and the probability of recapture; Lebreton et al. 1992), estimates of adult survival using this metric are difficult to interpret. Mark-recapture methods provide more reliable estimates of survival rates because they estimate apparent survival (ϕ) separately from the probability of re-sighting (p; Lebreton et al. 1992). While this allows inferences to be made regarding ϕ and p separately, care still needs to be taken in interpreting these two parameters as each is the product of two factors: site propensity and re-sighting probability in the case of p, and true survival and site fidelity in the case of ϕ. Prior demographic studies on shorebirds that applied mark-recapture methods found re-sighting rates to be < 1.0 (with some rare exceptions; e.g., Johnson et al. 2001) and to vary by sex, year, and age-class. Apparent survival rates were typically found to be lower in the year following initial capture than in subsequent years (Sandercock 2003), and females were often found to have lower apparent survival rates than males (e.g., Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000, Johnson et al. 2010, but see Paton 1994, Warnock et al. 1997). The latter finding may be because females actually survive less well or because they have higher emigration or dispersal rates than males.

Similarly, many estimates of shorebird chick survival have relied on methods that are difficult to make inferences from: return rates (e.g., Jönsson 1991) or counts of fledglings at the end of the season (e.g., Blomqvist and Johansson 1991). Patterns emerging from previous studies include: older chicks generally survive better than younger chicks (Soikkeli 1967, Schekkerman et al. 1998, Pearce-Higgins and Yalden 2002, Ruthrauff and McCaffery 2005), low temperatures negatively impact survival of chicks (Meltofte et al. 2007, Tulp 2007), high insect biomass positively affects chick

growth and survival (Schekkerman et al. 2003, Tulp 2007), high lemming densities are correlated with high chick survival (Summers and Underhill 1987, Blomqvist et al. 2002), and chicks hatching earlier in the season survive better than those hatching later (Soikkeli 1967, Ruthrauff and McCaffery 2005, Tulp 2007, Hartman and Oring 2009).

The *arcticola* subspecies of Dunlin (*Calidris alpina arcticola*), a small sandpiper, breeds on the arctic coastal plain of Alaska and western Canada and winters in Asia (Fernández et al. 2008). This subspecies is thought to be declining due to habitat destruction on the non-breeding grounds and declines of particular populations on the breeding grounds (Fernández et al. 2008). Consequently, the subspecies has been listed as a species of conservation concern in both the U.S. (U.S. Fish and Wildlife Service 2008) and Canada (Donaldson et al. 2000). To better understand what may be causing these declines, I investigated adult and chick survival of *arcticola* Dunlin breeding at Barrow, Alaska, USA. Breeding ecology data have been collected at six long-term study plots since 2003 wherein nests were monitored until hatch and adults were individually color-banded and re-sighted during the short breeding season (early June – late July). These data are essential for estimating demographic parameters, which for *arcticola* Dunlin, are currently unknown.

In chapter one, I investigated the survival of *arcticola* Dunlin adults using mark-recapture data collected between 2003 and 2010. Dunlin from this population show high site fidelity, and conducting this study on the breeding grounds allowed factors such as individual nest initiation date and nest success to be incorporated into the analyses. I examined the relationship of adult survival to a suite of covariates: sex, the timing of local spring snow melt, average nest success, individual nest success and nest initiation date, the presence of a glue-on radio transmitter, local predator control, and the completion of the Saemangeum Dike in South Korea. Apparent survival and re-sighting rates were estimated using Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965) in an information theoretic framework (Burnham and Anderson 2002).

In chapter two, I investigated the survival of *arcticola* Dunlin chicks between hatching and fledging in relation to age, insect biomass, hatch date, and temperature. I

also examined whether chick survival varied between first and replacement clutches using nests that were part of a concurrent study that experimentally investigated the frequency of re-nesting in this population (Gates 2011). Using nest survival models in an information-theoretic framework (Burnham and Anderson 2002), I determined which factors most affected daily survival rates and calculated the probability of surviving to 15 days of age. Previous studies of other avian taxa have reported mixed results of the effects of re-nesting on chick survival, with some studies showing a difference in survival between first and replacement nests (e.g., Verboven and Visser 1998, Arnold et al. 2004, Jamieson 2011), and others showing no difference (e.g., Yasué and Dearden 2008, Bettega et al. 2011).

The robust estimates of adult and chick survival rates for *arcticola* Dunlin generated by my study will allow us to better understand the potential role of these demographic parameters in the apparent decline of this subspecies. Further, identifying sources of variation in these estimates will assist in allowing the prediction of how this species might be impacted by future changes. For example, we could make more educated calculations as to how chicks may be affected by temperature or insect abundance changes predicted to result from global climate change.

CHAPTER 1

FACTORS AFFECTING ANNUAL SURVIVAL OF ARCTIC-BREEDING DUNLIN (*CALIDRIS ALPINA ARCTICOLA*)[1]

ABSTRACT

We used live encounter models to estimate apparent annual survival rates of arctic-breeding Dunlin (*Calidris alpina arcticola*) from 8 years of mark-recapture efforts near Barrow, Alaska, USA. Between 2003 and 2010, we marked 208 adult Dunlin (99 male, 109 female) with unique color-band combinations and re-sighted or recaptured them at nests in subsequent years. Using a two-step information-theoretic approach for model development and selection, we identified important explanatory factors. Our best approximating model indicated that re-sighting probabilities were higher for males (0.89, 95% CI: 0.82 – 0.93) than females (0.73, 95% CI: 0.61 – 0.82), and that survival was higher for males than for females, for birds initiating nests earlier rather than later, and varied by year. On average, survival probabilities were 0.60 (SE 0.04, range: 0.41 – 0.77) and 0.41 (SE 0.05, range: 0.23 – 0.60) for males and females, respectively. This difference may reflect reality or may be an artifact of higher emigration by females. Birds initiating nests just 10 days after the average initiation date for the population had an 11 – 31% reduction in their survival estimate. Adults laying nests earlier may be of higher quality and/or may benefit from completing the reproduction process earlier. Yearly survival estimates were highly variable. This study found that Dunlin adult survival rates were relatively low, indicating additional need to address potential threats to the species throughout its annual cycle. We recommend continued collection of survival data and a re-analysis in the future.

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INTRODUCTION

Around the world, many shorebird species appear to be declining, and for many species or populations the causes of declines are not known (Brown et al. 2001, Thomas et al. 2006, Bart et al. 2007). Identifying relationships between parameters such as fecundity and survival, as well as identifying factors thought to be impacting populations, provides invaluable information for directing conservation actions (e.g., Crouse et al. 1987). However, to determine what demographic rates are likely to affect population trends the most, those parameters need to be accurately estimated (Caswell 2001). Unfortunately, for many shorebird species we lack even the most basic demographic rates, largely due to difficulties in collecting the data necessary to estimate these rates (Sandercock 2003).

Small shorebirds typically begin breeding at age 1 or 2 (Summers et al. 1995, Colwell 2010), have moderate but highly variable productivity (Colwell 2010), and have moderate to high adult survival (Sandercock 2003). These characteristics often mean that reductions in adult survivorship can have large negative consequences to population growth rates (Hitchcock and Gratto-Trevor 1997, Sandercock 2003, Ottvall and Härdling 2005, Koivula et al. 2008). Baseline estimates of shorebird survival rates are limited and in some cases may be unreliable. Until recently, researchers have typically used simple return rates (i.e., the proportion of marked individuals that are recaptured or re-sighted in a subsequent year) as a measure of adult survival (Sandercock 2003, Colwell 2010). However, return rates are difficult to interpret and can be biased because true survival is the product of 4 parameters: true survival, site fidelity, site propensity, and the probability of recapture; but variation in the latter 3 components is not measured and is attributed to survival rate (Lebreton et al. 1992). Further, survival rates are potentially biased by low or high values of any of the other parameters, which would cause estimates of return rates, and thus survival, to be low or high (Martin et al. 1995). More reliable estimates of apparent survival rates (the product of true survival and site fidelity) using mark-recapture methods, which account for the probability of detection (the product of the detection rate and site propensity), are more robust, and allow further investigation of

potential factors affecting survival rates. Estimates using this methodology are now commonly used in conjunction with demographic models and provide powerful insights into population growth trends.

We estimated apparent survival rates of adult *arcticola* Dunlin (*Calidris alpina arcticola*), a small sandpiper (Scolopacidae; Warnock and Gill 1996) that appears to be declining (Fernández et al. 2008, Amano et al. 2010) and is listed as a species of conservation concern in both the U.S. (U.S. Fish and Wildlife Service 2008) and Canada (Donaldson et al. 2000). Reasons for this designation include declines in abundance on the breeding grounds (Arctic Coastal Plain of Alaska and western Canada) and loss of wintering and migration habitat in coastal Asia (Alaska Shorebird Group 2008, Fernández et al. 2008). Return rates (Heldt 1966, Soikkeli 1970a, Jönsson 1991, Thorup 1999) and apparent survival rates (Warnock et al. 1997, Schekkerman et al. 2004) have only been previously estimated for other subspecies of Dunlin. However, these apparent survival rates may be biased (e.g., Warnock et al. [1997] used an extremely long sampling period during which death occurred) or not long enough to detect yearly variation or trends (e.g. Schekkerman et al. [2004] produced estimates for only two years). Further, these estimates may not be indicative of *arcticola* Dunlin rates or trends, because this subspecies breeds and winters in different locations than populations of subspecies for which estimates have been made (del Hoyo et al. 1996).

Using Cormack-Jolly-Seber models (CJS; Cormack 1964, Jolly 1965, Seber 1965), we estimated apparent survival rates of adult *arcticola* Dunlin using capture-mark-recapture data collected between 2003 and 2010. We evaluated differences in apparent survival rates between males and females, and the relationship of apparent survival rates with factors potentially indicative of an individual's quality or condition (individual nest initiation date and individual nest success), as well as population-level factors (average nest success, timing of spring snow melt, levels of fox predation on the breeding grounds, and changing migratory stopover habitat availability).

METHODS

Study Area

We conducted this 8-year study near Barrow, Alaska (71°18″N, 156°45″W), on four (2003) to six (2004 – 2010) long-term study plots. Plots were 0.16 km^2 in 2003 and were expanded to 0.36 km^2 in 2004 (see Naves et al. 2008 for details). Average Dunlin nest density on these plots is ~16 nests/km^2 (R. B. Lanctot unpubl. data). Tundra habitat varies across these plots, from low wet areas to dry ridges and polygons dominated by grasses and moss (Brown et al. 1980). Fox control has been implemented in the Barrow area since 2005 in an effort to increase Steller's Eider (*Polysticta stelleri*) productivity.

Field Methods

Nest monitoring – Plots were searched daily for nests from early-June to mid-July in each year of the study. Nests were located by following adults back to their nest or by flushing adults using a rope-drag. If nests were found after a full clutch had been laid, nest initiation date was calculated by floating the eggs (Liebezeit et al. 2007) or back-calculating from day of hatch. Hatch dates were estimated by adding the incubation duration (21 days; Holmes 1966) to the date the fourth egg was laid. To determine nest fate, nests were checked every three to five days until four days before the estimated hatch date. Nests were then checked every two days until eggs began to show signs of hatch, and daily once eggs were starred. Nests were considered successful if at least one chick hatched. In each year, we calculated the percentage of Dunlin nests that were successful as the number of successful nests divided by the total number of nests monitored on all plots. We categorized years as low or high nest success years when less than or greater than 50% of nests survived to hatch, respectively.

Adult marking – Adults were captured on the nest using a bow-net (Bub 1995), and were marked with a U.S. Geological Survey metal leg band and a unique combination of Darvic® color bands. Band ends were soldered to reduce the likelihood of band loss. We weighed and took morphological measurements (culmen, total head, tarsus, wing, and weight) of all birds captured. We also collected a small amount of blood

from the brachial vein and used molecular techniques to sex individuals (see Gates 2011 for details). If molecular sexing was unavailable for an individual, we used a discriminant function model (DFM) based on morphological measurements (see Gates 2011 for details) to assign sex. If sex assignment using the DFM was ambiguous, we compared measurements of both individuals of a pair, and assumed the larger individual was the female (Warnock and Gill 1996, Gates 2011). Twenty-four males and four females were equipped with radio transmitters over two summers, 2008 and 2009. Radio transmitters (Model A2455, 1.2 g, Advanced Telemetry Systems, Isanti, Minnesota; or Model BD-2, 1.4 g, Holohil Systems Ltd., Ontario, Canada) were glued to the back on an area clipped of feathers approximately 1 cm above the uropygial gland (Warnock and Warnock 1993). Transmitters attached with glue typically stay on shorebirds for several weeks to several months (Warnock and Takekawa 2003), and would be expected to fall off prior to fall migration.

Covariate data – Most individuals (89%) were observed or captured at a nest site, providing individual covariate data for nest initiation date and nest success. For individual nest success, individuals not associated with a nest were given a value of success if greater than 50% of nests in that individual's study plot hatched, or fail if less than 50% of nests in that study plot hatched. For individual nest initiation date, individuals not associated with a nest were assigned the average initiation date of all Dunlin nests in that year. We categorized yearly spring snow melt as average or late based on whether the day of the season when snow cover was $\leq 50\%$ was before or after the average across the eight years of the study, respectively. Snow cover was estimated every two to three days as the average percent snow cover of thirty-six 50x50 m quadrats in each study plot. Quadrat percentages were then averaged across all plots to determine the date of $\leq 50\%$ snow cover.

Recaptures and re-sightings – Data on encounters of previously marked individuals were collected between early June and mid-July. Encounters consisted of physical captures of birds on nests and re-sightings of birds using spotting scopes or binoculars. Due to the large number of technicians re-sighting within and across years,

we considered birds present only if they were physically captured or had at least two re-sightings during a given year (Warnock et al. 1997). Hereafter we use the term re-sighting to refer to both recapture and re-sighting rates.

Data Analysis

Goodness-of-fit – We assessed goodness-of-fit (GOF; i.e., how well the data fits the global model) using three methods. First, we used program U-Care to examine the presence of heterogeneity (test 2) or transiency (test 3; Pradel et al. 1997, Choquet et al. 2009) in the data. Second, we used the bootstrap GOF test in program MARK (version 6.1; White and Burnham 1999) to calculate the variance inflation factor, $\hat{c}$. We calculated the bootstrap deviance and $\hat{c}$ estimates as the deviance for the global model divided by the average of deviance from 100 simulated data sets and the $\hat{c}$ for the global model divided by the average $\hat{c}$ for 100 simulated data sets, respectively. Finally, we removed all individual covariates from our data set and ran the median $\hat{c}$ test in program MARK.

Model set – We developed an *a priori* model set and used a two-step information-theoretic approach for model selection (Lebreton et al. 1992, Burnham and Anderson 2002). Models consisted of biologically relevant factors that we predicted could affect Dunlin re-sighting (p) and/or apparent survival (ϕ) probabilities. In addition, we included constant and year-dependent models for both p and ϕ. Below we describe the predicted effects of each factor (factor abbreviation in parentheses) separately for p and ϕ.

1. Sex (s) – (***p***) We predicted that males would have a higher re-sighting probability than females because they are present on the breeding site for a longer period of time and their behavior makes them more visible than females (Holmes 1966). Males arrive to the breeding site first, establish and defend a territory, attract females using aerial displays, and typically have the primary role in brood-rearing (Holmes 1966). Some studies have found higher re-sighting probabilities for males than females of other Dunlin subspecies (Jönsson 1991, Jackson 1994, Thorup 1999), however, other studies were inconclusive (Heldt 1966, Soikkeli 1970a, Schekkerman et al. 2004). (**ϕ**) We

predicted that apparent survival would be lower for females because they invest more energy in reproduction than males, and so have a higher trade-off between reproduction and survival (Jönsson and Alerstam 1990). Females are also more likely to emigrate from the study area if they lose their mate or divorce after nest failure (Soikkeli 1970b, Gates 2011), thereby reducing apparent survival. Return rates have not been found to differ by sex in other Dunlin subspecies (Heldt 1966, Soikkeli 1970a, Warnock et al. 1997, Schekkerman et al. 2004, but see Jönsson 1991). Previous studies on other Scolopacidae sandpipers have reported mixed results; some found higher survival of males (Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000, Johnson et al. 2010, Pakanen et al. 2010) while others did not (Sandercock et al. 2000, Brochard et al. 2002).

2. Timing of Spring Snow Melt (sm) – We used a categorical variable for this factor, average or late, based on the date of $\leq 50\%$ area-wide snow cover. ($\boldsymbol{p}$) We predicted that re-sighting probabilities would be higher in seasons with early or average timing of spring snow melt and lower in seasons with late spring snow melt. Breeding probability may be lower in years with late spring snow melt (Meltofte et al. 2007), thereby likely reducing the chance an individual stays in the study area and is detected in a given year. ($\boldsymbol{\phi}$) We predicted that survival would be lower the year following a late spring snow melt than the year following an early or average spring snow melt. Later nest initiation in years with late spring snow melt (Green et al. 1977, Meltofte et al. 2007, Smith et al. 2010) leaves less time at the end of the season to prepare for southbound migration, potentially leading to higher mortality during migration (see also "individual nest initiation date"). Few studies have investigated this but Gratto et al. (1985) found that Semipalmated Sandpipers had lower return rates following very late snow melt years.
3. Population-level Nest Success (ns) – We used a categorical variable for this factor, high or low, based on years of average hatch success above or below

50%. (***p***) We predicted that re-sighting probabilities would be higher in seasons with high Dunlin nest success than in seasons of low nest success. When nests survive to hatch, birds are present for a longer period of time, allowing more time for nests to be found and the associated adults to be identified. (**ϕ**) We predicted that apparent survival rates would be lower following seasons of high nest success than after seasons of low nest success. When nest success is high, males and females invest more time, resources, and energy in reproduction and may have less time to replenish body reserves needed for migration, potentially resulting in a higher cost of reproduction and thereby lower survival.

4. Individual Nest Success (is) – This factor was an individual covariate with binary values, success or failure. (***p***) We did not consider the effect of this variable on *p*. (**ϕ**) We predicted that apparent survival would be lower for individuals whose nest successfully hatched for the same reasons as stated for "population-level nest success".
5. Individual Nest Initiation Date (id) – Individual nest initiation date was an individual covariate with continuous values for the date of the season that the individual's nest was initiated. (***p***) We did not consider the effect of this variable on *p*. (**ϕ**) We predicted apparent survival would decline with nest initiation date. Individuals nesting earlier are often presumed to be of higher quality (e.g., more experienced, more efficient at finding resources, better able to obtain high quality territories) than individuals nesting later (Heldt 1966, Soikkeli 1967, Gratto et al. 1983, Thompson et al. 1986, Johnson and Walters 2008). Higher quality or condition could increase the survival of individuals arriving earlier. Individuals arriving later also likely nest later and would have less time to prepare for southbound migration at the end of the season.
6. Fox Control (f) – We used a categorical variable for this factor, present or absent, depending on whether or not fox control was conducted in a given year. (***p***) We predicted that re-sighting rates would be higher in seasons with

fox control (2005–2010) than in seasons without fox control (2003 and 2004) because nest success was generally higher in years with fox control (see justification for "population-level nest success"). (ϕ) We predicted that apparent survival would be lower in the year following a season with fox control. Nest and fledging success are expected to be higher in seasons with fox control, leading to lower apparent survival for the same reasons as stated for high "population-level nest success".

7. Saemangeum Dike (d) – We used a categorical variable for this factor, before or after, for years before or after the Saemangeum Dike was completed. A high rate of land reclamation in Asia, and the associated reduction of sediment discharge on river deltas and mudflats, is thought to have reduced the availability of important migration stopover and wintering sites for Dunlin (Cao et al. 2009). A prominent recent land reclamation was the 2006 completion of the Saemangeum Dike in South Korea, which reclaimed 401 km^2 of intertidal mudflats used by staging Dunlin during migration (Moores et al. 2008). A reduction in the number of Dunlin using the area after the completion of the dike has been reported (Moores et al. 2008). Re-sightings of Dunlin banded in Barrow in the vicinity of the Saemangeum Dike confirm that at least part of our study population utilizes this area for at least part of the non-breeding season (R. B. Lanctot, unpubl. data). (p) We did not expect re-sighting rate to be affected by the Saemangeum Dike because it seemed unlikely its completion would cause birds to emigrate or forgo breeding at our site. (ϕ) We predicted that Dunlin would have lower apparent survival in the years following completion of the Saemangeum Dike (2006 – 2010) than in years before completion of the dike (2003 – 2005). The loss of these important habitats likely resulted in Dunlin spending more time searching for suitable foraging habitat, potentially resulting in reduced overwinter or migratory survival. We examined three variations of the dike variable. In all versions the pre-dike period was held constant and the post-dike period was: 1) constant;

2) a time trend; or 3) divided into two separate periods, 2006 – 2007 and 2008 – 2010. We did not assess whether males and females were affected differently by the presence of the dike because there was no information on how the sexes distributed themselves on migration or wintering areas.

8. Radio Transmitter (r) – We used a categorical variable for this factor, present or absent, depending on whether or not an individual received a radio transmitter in a given year. (***p***) By definition, individuals that received a radio transmitter were captured and so had a probability of capture of 1 in that year. Because this affected a small number of birds we did not consider this in modeling. (**ϕ**) We predicted that Dunlin carrying a radio transmitter would have lower apparent survival in the year following application of the transmitter than Dunlin without a transmitter. A transmitter is expected to increase energy requirements due to the increased weight and reduced aerodynamic profile, and may hinder the ability to obtain resources before or during migration. For example, Upland Sandpipers (*Bartramia longicauda*) fitted with a leg harness had lower return rates than those without a radio (Mong and Sandercock 2007). We did not model the effect of sex with radio transmitters as transmitters were mostly deployed on males.

Model development and selection criteria – We developed model sets for p and ϕ separately. For our evaluation of p, we examined each factor alone, including constant and year models, and each factor with an additive and interactive effect of sex. We had a total of 14 models for p. For our evaluation of ϕ, we examined each factor alone (including the constant and year models and all 3 formulations for dike – see "dike" factor description above), and additive and interactive 2-way effects of sex and individual covariates (is, id, r) with all other factors except dike formulations 2 and 3, and the combination of sex and either dike or radio transmitter. We also examined each of these 2-factor models, except those that already included sex, with an additional additive and interactive effect of sex. We had a total of 103 models for ϕ.

We used program MARK for the two-step model selection process. We first determined which factor(s) best fit the data for p using only the interactive effect of sex and year for apparent survival (ϕ_{s*y}). In the second step, the model best explaining variation in the data for p was used for all models examining which factors best explained variation in the data for ϕ. For each step, models were ranked using Akaike's Information Criterion (AIC) corrected for sample size and overdispersion ($QAIC_c$; Burnham and Anderson 2002). Models within 2 $QAIC_c$ units of the model with the lowest $QAIC_c$ value were considered as having considerable support for explaining variation in the data (after removing models with uninformative parameters, where warranted; Burnham and Anderson 2002, Arnold 2010). We determined factor support by summing model weights for each factor over all models and rescaling the results so that the summed model weight for the most supported factor was equal to 1.0.

RESULTS

The average date of ≤ 50% snow cover was 8 June (± 1.6 days SE). In six years the spring snow melt date was classified as average, but in two years, 2005 and 2010, the snow melt date was classified as late, as it occurred 4 and 8 days later than the average date, respectively. The average apparent hatch success across all years was 59.3% ± 9.2% SE. Three years, 2003, 2004 and 2009, were classified as low nest success years, and all other years were classified as high nest success years. The average initiation date for all years was 12 June (range: 3 June – 1 July).

A total of 208 adult Dunlin were banded on our plots from 2003 to 2009: 99 males and 109 females. All but six birds (< 3%) were sexed using molecular techniques. Of all individuals banded, 49.5% returned to the study area at least once, with males returning more often (55.5%) than females (44.0%). We re-sighted between 3 and 23 males and between 3 and 18 females in any given year (Table 1.1).

Five individuals were right-censored because, as part of related studies, they: 1) were re-banded with an alpha-numeric flag (which faded over time) and no individual color bands; 2) were re-banded with four bands on the tibiotarsus; 3) were observed with

a leg injury, possibly due to marking; or 4) received a harness-type backpack. The first three factors made subsequent re-sightings difficult and the last two factors potentially reduced survival due to research activities.

Goodness-of-fit – We did not detect any evidence of heterogeneity in re-sighting probabilities (overall $P = 1.00$ for males, 0.98 for females) or transiency in either sex (overall $P = 0.84$ for males, 0.91 for females). Bootstrap GOF results indicated that the data were only slightly overdispersed. The deviance of the global model divided by the mean deviance of the simulated data sets was 1.02. The $\hat{c}$ of the global model divided by the mean $\hat{c}$ of the simulated data sets was 0.85. The median $\hat{c}$ procedure produced a $\hat{c}$ estimate of 0.99 (95% CI: 0.97 – 1.01). To be certain overdispersion was accounted for, we adjusted the $\hat{c}$ of all of the models in our set using the most conservative value: 1.02.

Model selection – The top model for explaining re-sighting probability (p) included sex (p_s) as an explanatory factor. The model with an additive relationship between sex and population-level nest success (p_{s+ns}; Step 1, Table 1.2), also appeared to have substantial support, with a $\Delta QAIC_c$ value of 0.18. However, the addition of population-level nest success lowered the model deviance by only a small amount and the confidence interval of the coefficient value for this variable nearly encompassed zero (β_{ns} = -0.68, 85% CI: -1.35 – -0.00), suggesting this was an uninformative parameter. Models including any other factors, or factor combinations, did not receive much support, having $\Delta QAIC_c$ values greater than two. Therefore, we used only p_s to evaluate apparent survival models.

For apparent survival (ϕ), three models had $\Delta QAIC_c$ values less than two (Step 2, Table 1.2). These models included sex, individual nest initiation date (id), individual nest success (is), and year (y) as explanatory factors ($\phi_{s+id+y}\, p_s$, $\phi_{s*id+y}\, p_s$, and $\phi_{s*is+y}\, p_s$). Model weight sums for all factors were: sex = 1.0, individual nest initiation date = 0.80, year = 0.62, individual nest success = 0.39, timing of spring snow melt = 0.19, fox control = 0.13, radio transmitter = 0.10, population-level nest success = 0.09, and the completion of the Saemangeum Dike = 0.07. These weights suggest that sex and individual nest initiation date were the most important variables in our model set. To

evaluate whether uninformative parameters were present in these models, we examined the beta values and 85% confidence intervals for these factors as well as their relative importance (i.e., model weight; Arnold 2010). Adding individual nest initiation date to the model with additive effects of sex and year (a comparison of models 1 and 5; Step 2, Table 1.2) reduced the model deviance a considerable amount. Further, the confidence interval for the individual nest initiation date coefficient did not encompass zero (β_{id} = -0.05, 85% CI: -0.08 – -0.01), and this variable was our second most supported factor by model weight. We therefore had no reason to consider individual nest initiation date as an uninformative parameter in model 1. A comparison of models 1 and 2 indicated that the interaction term of sex and individual nest initiation date (s*id) reduced model deviance by only a small amount (Step 2, Table 1.2) and the confidence interval for the s*id interaction term coefficient encompassed zero (β_{s*id} = 0.04, 85% CI: -0.03 – 0.11). Therefore, we considered this interaction term to be an uninformative parameter. Although model 3, $\phi_{s*is+y}\, p_s$, had considerable support ($\Delta QAIC_c$ = 1.60), the summed model weight for individual nest success was lower than for sex, individual nest initiation date and year; and this model contained an interaction term not included in model 1, which can make interpretation of model-averaged estimates difficult. Therefore we chose to use the top model only to generate estimates of p and ϕ.

Parameter estimates – Average estimates of apparent survival across years and initiation dates were 0.60 ± 0.04 (range: 0.41 – 0.77) for males and 0.41 ± 0.05 (range: 0.23 – 0.60) for females. Survival probabilities were higher for males than females in all years (β_s = 0.79 ± 0.23; Fig. 1.1), and declined with increasing nest initiation date (β_{id} = -0.05 ± 0.02; Fig. 1.2). Re-sighting probabilities were lower for females (0.73, 95% CI: 0.61 – 0.82) than for males (0.89, 95% CI: 0.82 – 0.93).

DISCUSSION

We used Cormack-Jolly-Seber models to estimate apparent survival rates of *arcticola* Dunlin breeding at Barrow, Alaska. Our predictions for the effect of the factors we evaluated on survival rates were based on the implications of each factor for either a

bird's condition or quality when arriving at the breeding grounds, and/or the level of investment in breeding and the subsequent consequences for a bird's condition during migration. Assuming this premise is valid, timing of nesting and, to a lesser extent nest success, appear to provide the best characterization of breeding investment. The high importance of individual measures (nest initiation date and nest success) suggests that individual characteristics (e.g., condition, experience, foraging efficiency) are important in determining the cost of reproduction that an individual experiences. It also suggests that individual variation in reproductive costs is large enough that population averages of breeding measures (e.g., population-level nest success) do not adequately characterize breeding investment for the purpose of assessing impacts on survival.

Apparent Survival Rates

Sex – As predicted, apparent annual survival rates were higher for males than for females. This pattern has been found previously in only one study of Dunlin that used return rates (Jönsson 1991); although this could be due to differences in re-sighting rates. Other Dunlin studies using return rates or apparent survival estimates have not found this difference (Heldt 1966, Soikkeli 1970a, Warnock et al. 1997, Schekkerman et al. 2004). Lower survival rates of females have been documented in other shorebird species, including Semipalmated and (*Calidris pusilla*, Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000) and Western Sandpipers (*C. mauri*, Johnson et al. 2010). This pattern may be due to the higher energetic costs associated with reproduction for females and the possible negative affect this has on overwinter survival. In contrast, the reproductive costs for males may be quite low, especially for older birds that reunite with mates of prior years (Lanctot et al. 2000). Although males typically tend the chicks (B. L. Hill pers. obs.), requiring them to stay in the breeding area 2 – 3 weeks longer than females, nest failure may limit the average energetic cost this represents, whereas egg production represents a larger and more fixed cost for females. This may be particularly evident when females lay a replacement clutch after nest failure, which commonly occurs in this population (Gates 2011). Re-nesting has been shown to affect overwinter survival

in other species. For example, Nilsson and Svensson (1996) found that female Blue Tits (*Parus caeruleus*) that laid replacement clutches had lower overwinter survival, which they suggested was likely due to the production of low quality feathers following breeding, which in turn increased thermoregulatory costs. Dunlin in our area molt during breeding, and though unknown, females could experience a similar trade-off between the energetic costs of egg production for a second clutch and feather quality, and as a result suffer negative effects on survival. Other differences between the sexes, such as migration strategies or access to preferred habitats on migration or wintering sites, may also contribute to sex differences in survival rates (Durell 2000).

Our lower apparent survival rate for females may, at least in part, represent a higher rate of permanent emigration than males, rather than reflecting a difference in true survival. Females are more likely to move to a nesting site off of a study plot following nest failure and divorce or loss of a mate within a season (Gates 2011). This would result in permanent emigration if the individual continued to nest off the study site in subsequent years. Jackson (1994) and Thorup (1999) studying *schinzii* Dunlin found that dispersal from previous breeding sites was female-biased, and this pattern has also been observed for Semipalmated (Sandercock et al. 2000, Jehl Jr. 2006) and Western Sandpipers (Sandercock et al. 2000). Further study is needed on divorce and movement rates to evaluate their effects on apparent survival rates (e.g., Cilimburg et al. 2002). One way to evaluate the contribution of permanent emigration to apparent survival rates is to examine re-sightings of marked birds away from the breeding grounds (e.g., Stenzel et al. 2007). Five Dunlin (3 male, 2 female) marked at our study site were observed on the wintering grounds in Asia after failing to be seen at our study site in the previous summer but this data is inadequate to examine permanent emigration.

Individual nest initiation date – As predicted, apparent survival rates declined with nest initiation date. Neville (2002) found that female Western Sandpipers whose young hatched earlier had higher return rates than those whose young hatched later. Dunlin that breed earlier may have higher survival because this nesting phenology allows greater access to resources prior to and during migration, or, earlier breeding could

indicate that these birds are in better condition or by some measure are of higher "quality" (e.g., are more experienced, more efficient at foraging, or they secure better territories) prior to breeding. The earlier a clutch hatches (in the case of females) or a brood fledges (in the case of males), the more time an individual has to prepare for migration, which would be expected to translate to higher survival rates during migration. Also, if late nesting Dunlin migrate later, they may only have access to limited food resources if prey depletion occurs at migratory stopover areas (e.g., Schneider and Harrington 1981). This has been shown in Red knots (*C. canutus*), where individuals that arrived later to a stopover site were lighter (suggesting poorer condition) and survived less well than those arriving earlier (Baker et al. 2004). Sandpipers that initiate nests early are often returning breeders (Heldt 1966, Soikkeli 1967, Gratto et al. 1983, Thompson et al. 1986, Lanctot et al. 2000, Johnson and Walters 2008). Experienced birds such as these typically pair quickly (avoiding costly mate attraction displays; Lanctot et al. 2000) and likely benefit from knowledge of favorable foraging locations (Oring and Lank 1984) that may enable them to maintain better condition during breeding and ultimately to survive better. Finally, a later initiation date may indicate that this is a replacement nest for an individual. If so, the pair likely incurred additional costs to reproduction (see "Sex" discussion).

Year – We found that apparent annual survival rates varied by year, as is often the case with shorebirds (Sandercock 2003). However, we note that this relationship could have been driven primarily by very low survival in the first year of the study. Yearly variation in survival rates could be attributed to any number of factors we did not consider, such as predation pressure (e.g., Dekker and Ydenberg 2004), toxins or parasites (e.g., Buehler et al. 2010), contaminants (e.g., Warnock and Schwarzbach 1995), habitat loss or alterations (e.g., Burton et al. 2002), food abundances (e.g., Schneider and Harrington 1981), and weather (e.g., Davidson and Evans 1982) – all of which could vary annually on the breeding and/or wintering grounds, or along the migration route. Sources of mortality have been recorded throughout the annual cycle for many shorebirds (Brown et al. 2001, Butler et al. 2004). However, for *arcticola* Dunlin, it

is thought that threats that potentially impact survival are greater during the non-breeding season than during the breeding season (Fernández et al. 2008). Unfortunately, data are not available to evaluate the effects of non-breeding season factors.

Factors with little or no support – Our predictions for the effect of population-level nest success, timing of spring snow melt, fox control, and the completion of the Saemangeum Dike on survival rates were not upheld. However, it is possible that our data were insufficient for detecting effects of these factors. We were surprised the Saemangeum Dike was not important for explaining variation in survival rates. While the Saemangeum Estuary still supports lower numbers of Dunlin (N. Moores pers. comm.), many were forced to find new foraging and roosting areas, and likely expended more energy than usual in the process (e.g., Rogers et al. 2006). While stopover lengths and major overwinter sites are largely unknown for *arcticola* Dunlin, the high rate of reclamation throughout the East Asian-Australasian flyway (e.g., Birds Korea 2010, Yang et al. 2011) may be enhancing intraspecific competition and thus impacting survival (Bamford et al. 2008, Cao et al. 2009).

Re-sighting Rates

Sex – Our prediction that males would have higher re-sighting probabilities than females was supported by our data. This difference is most likely because males are more visible than females during the early part of the breeding season, as they conduct displays to attract mates and defend territories (Holmes 1966, Lanctot et al. 2000, Schekkerman et al. 2004), and because males are typically present in the vicinity of the nest site for a longer period of time because they assume the primary brood-rearing role (B. L. Hill pers. obs.). In contrast, females appear to spend their time foraging prior to laying, an activity that makes them less noticeable (B. L. Hill pers. obs.). Females also typically leave the breeding site sooner than males because they don't participate in brood rearing for more than a few days, on average (B. L. Hill unpubl. data). A small proportion of females are also likely to move off the plot following nest failure if they divorce their mate. Gates (2011) found that female Dunlin at our study site that lost their initial nest

and divorced their mate always moved to a new nesting site (up to 8.1 km away) to lay a replacement clutch, whereas males always remained on their initial territory. Lower re-sighting rates of females have been found in other shorebirds (Holmes 1971, Gratto et al. 1985, Paton 1994), and females of several species have been documented to disperse further than males between seasons (Soikkeli 1967, Gratto et al. 1985, Jackson 1994, Clarke et al. 1997, Thorup 1999).

Factors with little or no support – Our predictions of an effect of population-level nest success, timing of spring snow melt, and fox control on re-sighting probabilities were not supported by our data. Although the effect size for these factors would have needed to be reasonably large to be detected by our relatively small data set, the lack of support for models containing these factors even though nest success was highly variable suggests they were not important for estimating re-sighting probabilities in this population.

Conclusions

This study allowed us to investigate several factors that may affect adult Dunlin survival. Our most interesting finding was that adult survival was lower for birds that initiated nests later. This could be because individuals that breed earlier are of higher quality or are in better condition than those that breed later, and/or because there is a higher cost of reproduction for individuals breeding later. Results of our modeling favored individual qualities (individual nest initiation date, individual nest success) over population-level variables (nest success, fox control, timing of spring). This suggests that individual quality plays an important role in survival or the cost of reproduction, or that population-level measures of breeding characteristics are inadequate for describing the cost of reproduction.

We found a fairly low rate of female survival, which could be limiting population growth. However, additional study is needed to determine if true female survival is low or if our apparent survival rates contain a higher emigration component than for males. Survival rate was variable among years; most noticeably survival was very low in the

first year of the study. We did not find any evidence that construction of the Saemangeum dike affected survival rates. However, our focus on this single site, or our binary classification of this variable as before and after completion of the dike, may have been an inadequate representation of habitat loss in this region. Predicted continued loss of intertidal areas in Asia (e.g., Yang et al. 2011), the most readily identifiable threat to this species, is still cause for concern. A re-evaluation of survival rates for this population should be conducted in several years to determine if apparent survival has declined.

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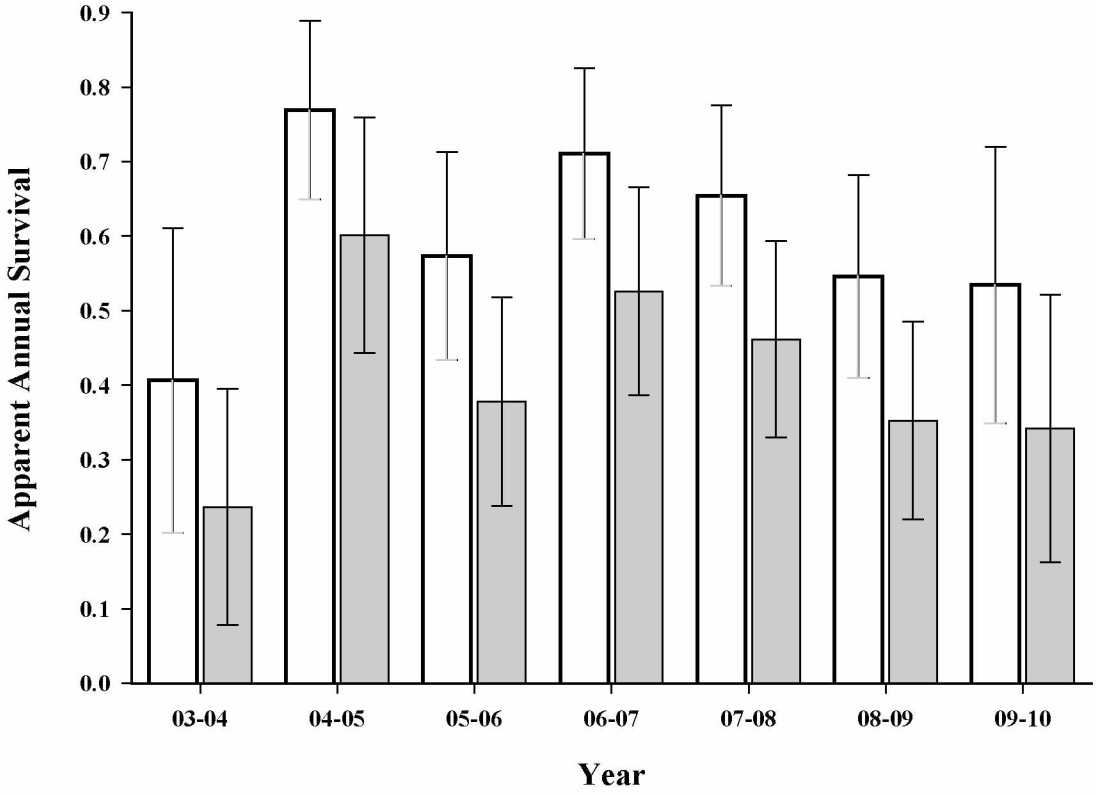

Figure 1.1. Estimates and 95% confidence intervals for apparent annual survival of male (black) and female (gray) adult Dunlin. Estimates are derived from top model (ϕ_{s+id+y}, p_s), which modeled additive effects of year, sex, and an individual covariate for nest initiation date. Estimates are calculated for the average nest initiation date for each year.

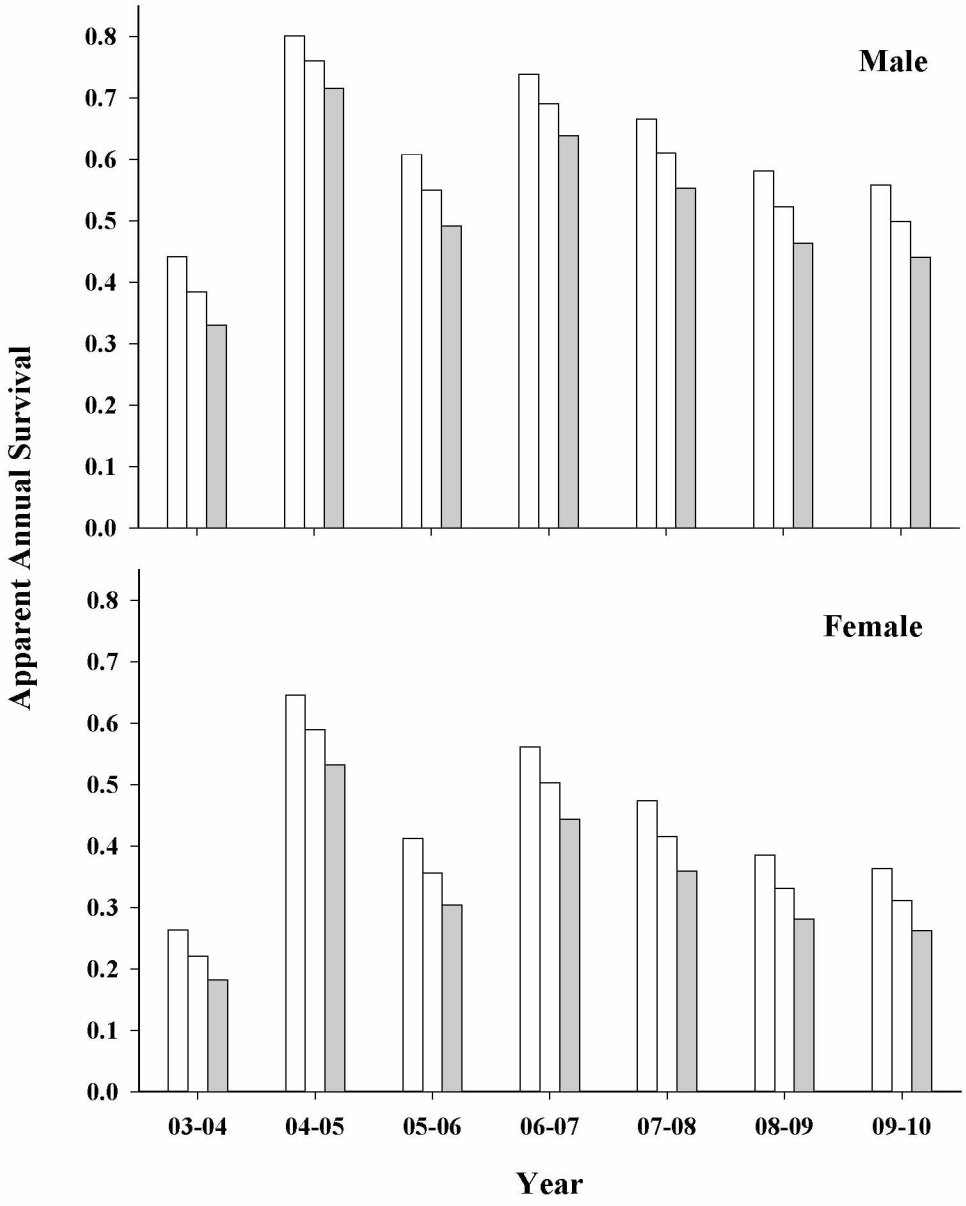

Figure 1.2. Estimates of apparent annual survival of male and female adult Dunlin at three nest initiation dates. Estimates are derived from the top model (ϕ_{s+id+y}, p_s), which modeled additive effects of year, sex, and an individual covariate for nest initiation date. Three initiation dates are shown: 9 June (black), 14 June (white), and 19 June (gray).

Table 1.1. Number of male and female Dunlin banded at nest sites at Barrow, Alaska, between 2003 and 2009, and the number of birds from each cohort re-sighted or recaptured in each subsequent year.

			# Re-sighted in subsequent years						
	Year	# banded	2004	2005	2006	2007	2008	2009	2010
Male	2003	14	3	3	2	2	1	1	2
	2004	20		13	11	7	7	5	4
	2005	15			7	6	2	1	0
	2006	17				8	6	1	2
	2007	13					7	4	3
	2008	13						7	3
	2009	7							4
	Subtotal	99	3	16	20	23	23	19	18
Female	2003	12	3	1	1	1	1	0	0
	2004	20		10	3	5	2	0	0
	2005	13			3	0	1	0	0
	2006	22				9	6	2	3
	2007	20					8	3	2
	2008	13						4	1
	2009	9							1
	Subtotal	109	3	11	7	15	18	9	7
	Total	**208**	**6**	**27**	**27**	**38**	**41**	**28**	**25**

Table 1.2. Model selection results for Cormack-Jolly-Seber survival analyses to determine the best re-sighting probability (p) model and the best apparent annual survival (ϕ) model for adult Dunlin. Models are ranked in ascending order by their Akaike's Information Criterion scores, adjusted for sample size and overdispersion ($QAIC_c$; $\hat{c}$ = 1.02). ϕ was modeled as a function of the interaction of sex and year for determining the best approximating model for p (step 1). The best model for p (as a function of sex), was used for all models evaluating the best approximating model for ϕ (step 2). Factors tested include individual nest initiation date (id), individual nest success (is), sex (s), year (y), population-level nest success (ns; high or low), fox control (f; present or absent), timing of spring snow melt (sm; average or late), and no effect (i.e., constant; c). See text for a description of the model set. Only models with $\Delta QAIC_c < 4.0$ are listed.

No.	Model	$\Delta QAIC_c$[1]	$QAIC_c$ wt.[2]	K[3]	QDeviance[4]
Step 1: Modeling re-sighting probability (p)					
1	$\phi_{s*y}\, p_{s}$	0.00	0.31	16	668.88
2	$\phi_{s*y}\, p_{s+ns}$	0.18	0.29	17	666.88
3	$\phi_{s*y}\, p_{s+f}$	2.18	0.11	17	668.87
4	$\phi_{s*y}\, p_{s+sm}$	2.18	0.11	17	668.87
5	$\phi_{s*y}\, p_{s*ns}$	2.31	0.10	18	666.80
Step 2: Modeling apparent survival (ϕ)					
1	$\phi_{s+id+y}\, p_{s}$	0.00	0.15	11	670.52
2	$\phi_{s*id+y}\, p_{s}$	1.49	0.07	12	669.88
3	$\phi_{s*is+y}\, p_{s}$	1.60	0.07	12	669.99
4	$\phi_{y}\, p_{s}$	2.58	0.04	09	677.33
5	$\phi_{s+y}\, p_{s}$	2.96	0.04	10	675.60
6	$\phi_{s+id}\, p_{s}$	3.23	0.03	05	686.30
7	$\phi_{s+is+y}\, p_{s}$	3.31	0.03	11	673.83
8	$\phi_{c}\, p_{s}$	3.57	0.03	03	690.73
9	$\phi_{s*is*id}\, p_{s}$	3.78	0.02	10	676.41
10	$\phi_{id+sm*s}\, p_{s}$	3.83	0.02	07	682.76

[1]Difference in $QAIC_c$ values between the current and top model.

[2]Model weight.

[3]Number of parameters.

[4]Quasi-likelihood deviance

CHAPTER 2

FACTORS AFFECTING CHICK SURVIVAL OF ARCTIC-BREEDING DUNLIN (*CALIDRIS ALPINA ARCTICOLA*) FROM INITIAL AND REPLACEMENT NESTS[1]

ABSTRACT

Productivity of arctic-breeding Dunlin (*Calidris alpina arcticola*) is affected by re-nesting propensity, and in turn, the affects that timing of nesting has on subsequent chick survival. We monitored 131 chicks by following adults and their broods using radio telemetry at Barrow, Alaska, USA, during the 2008 and 2009 breeding seasons. Chicks from 1) initial, 2) early replacement, and 3) late replacement nests were monitored until death or survival to 15 days of age. Replacement nests were located (after experimentally removing clutches from a sample of initial nests, either early or late in incubation) by radio-tracking the parents to their second nest. We estimated chick survival using nest survival models in program MARK. Chick survival was most affected by hatch date, chick age, and insect biomass. Daily survival rate (DSR) increased as insect biomass increased across all ages and hatch dates. However, DSR had complicated relationships with hatch date and age, as the top model included quadratic and interaction terms for these variables. Chicks from initial nests had a higher probability of surviving to 15 days of age (0.71 ± 0.07) than chicks from early (0.23 ± 0.19) or late (0.03 ± 0.61) replacement nests. Replacement nests have low productivity and should not be considered equivalent to initial nests when calculating recruitment estimates.

[1]Formatted for submission to the *Journal of Avian Biology* as: Hill, B. L., R. B. Lanctot, and C. M. Hunter. Factors affecting chick survival of arctic-breeding Dunlin (*Calidris alpina arcticola*) from initial and replacement nests.

INTRODUCTION

Forty-eight percent of the world's 200 shorebird species, and over half of the 50 shorebird species that breed in North America, are declining (Brown et al. 2001, Thomas et al. 2006, Bart et al. 2007). The causes of these declines are rarely known, but likely result from multiple factors such as changes in habitat, anthropogenic disturbance, predator abundance, environmental contaminants, or disease prevalence (Butler et al. 2004). These factors can affect demographic parameters such as survival and productivity (e.g., Burton et al. 2006, Pearce-Higgins et al. 2010), which in turn combine to determine population status and change.

The relative contribution of demographic parameters to population growth of shorebirds likely follows the general pattern for a typical avian life cycle, wherein adult survival is moderately high and reproductive output is variable (Stearns 1992, Sæther et al. 1996). This typically means that a change in adult survival will have a greater effect on population growth than an equivalent change in productivity or juvenile survival (Hitchcock and Gratto-Trevor 1997, Sæther and Bakke 2000, Ottvall and Härdling 2005, Koivula et al. 2008). However, a large change in productivity could have a similar effect on population growth as does a small change in annual survival. Reliable estimates of both survival and productivity parameters are important to evaluating their influence on population trends.

Of the major components of shorebird productivity (e.g., probability of breeding, nest success, probability of re-nesting, and pre- and post-fledgling survival), nest success is generally the most studied, as those data are easiest to collect. Survival of pre-fledgling chicks (hereafter referred to as chick survival) is seldom studied because of logistical challenges, especially in species with precocial young where chicks leave the nest site within hours of hatching (Holmes 1966a), are frequently highly mobile (e.g., Lanctot 1994), are often difficult to observe (e.g., Jamieson 2011), and typically hide or remain motionless in the presence of a predator (or researcher; Colwell 2010). In addition, timing and cause of death are usually unknown, as dead chicks are almost impossible to find.

Although about 30% of individual shorebirds worldwide breed in Arctic regions (Lanctot 2006), chick survival studies from these areas are especially sparse (but see Meltofte et al. 2007). The remote, large scale, and often inaccessible nature of these regions amplifies the expense and logistical challenges of such studies.

Nevertheless, previous studies of shorebird chick survival from the Arctic and elsewhere have identified several patterns. First, younger chicks usually have lower survival than older chicks (Soikkeli 1967, Schekkerman et al. 1998, Pearce-Higgins and Yalden 2002, Ruthrauff and McCaffery 2005). Second, low temperatures can negatively impact survival, especially in young chicks (Meltofte et al. 2007, Tulp 2007). This is supported by studies that observed fewer juveniles on the non-breeding grounds after colder summers (Beale et al. 2006, Soloviev et al. 2006). Third, chick survival and growth are positively related to insect abundance (Schekkerman et al. 2003, Tulp 2007), which is known to vary across a season (MacLean and Pitelka 1971, Tulp and Schekkerman 2008). Finally, in years of low lemming numbers, chicks often have lower survival, which is thought to be because predators switch from a diet of lemmings to one of avian eggs and chicks (Summers and Underhill 1987, Blomqvist et al. 2002). An important aspect of shorebird chick survival that has not been addressed is whether survival of chicks from re-nesting attempts differs from survival of chicks from first nesting attempts. Studies comparing chick survival from initial and replacement nests in other avian species have found mixed results (Verboven and Visser 1998, Hipfner 2001, Arnold et al. 2004, Yasué and Dearden 2008, Bettega et al. 2011, Jamieson 2011). However, shorebird studies wherein chick survival decreased across a season (Soikkeli 1967, Ruthrauff and McCaffery 2005, Tulp 2007, Hartman and Oring 2009) suggest that chicks from re-nesting attempts (i.e., later hatching nests) do not fare as well.

We investigated survival of chicks from first and replacement nests of Dunlin (*Calidris alpina arcticola*) breeding on Alaska's North Slope. We capitalized on an existing study in which a sample of initial (first) nests were experimentally removed and the attending adults followed via radio telemetry to determine rates of re-nesting (Gates

2011). Our study estimated the survival probability of chicks from hatching to 15 days of age and determined whether survival is related to chick age, insect biomass, hatch date, year, or temperature. Based on the results of prior studies, we predicted that chick survival would be positively correlated with age, insect biomass, and temperature, and negatively correlated with hatch date. The latter prediction would result in chicks from initial nests having higher survival rates than chicks from replacement nests. To our knowledge, this is the first shorebird study in the Arctic wherein chicks from a large number of known replacement nests were radio-tagged and monitored.

Our study was complicated by the fact that the U.S. Fish and Wildlife Service removed arctic fox (*Alopex lagopus*) from our study area in an effort to increase the productivity of threatened Steller's Eiders (*Polysticta stelleri*). We recognize that a study in the absence of a top shorebird nest predator (Summers et al. 1998, Liebezeit and Zack 2008, McKinnon and Bêty 2009) may cause our chick survival estimates to be higher than in an area with fox. However, this feature resulted in high shorebird nest hatching success (a necessary feature for a chick survival study), which was as low as 20% prior to fox control (R. B. Lanctot unpubl. data). In addition, arctic fox abundance (Summers et al. 1998, Smith et al. 2010) and predation of nests or chicks (Blomqvist et al. 2002, Liebezeit et al. 2009) are highly variable, both spatially and temporally, and our study conditions may be similar to other natural conditions where fox are scarce.

METHODS

Study Species

The *arcticola* Dunlin breeds in northern Alaska (and possibly into northwestern Canada) and winters in Asia along the coasts of China, Japan, Taiwan, and North and South Korea (Fernández et al. 2008). This subspecies is thought to be declining (Fernández et al. 2008, Amano et al. 2010), and has been listed as a species of conservation concern in both the U.S. (U.S. Fish and Wildlife Service 2008) and Canada (Donaldson et al. 2000).

Dunlin are a monogamous, ground-nesting shorebird that normally lay a 4-egg clutch. While both parents incubate, females typically desert a few days after hatch, leaving the male to rear the brood. The young are precocial, leaving the nest within a few hours after the last egg hatches. The adults aid in chick thermoregulation, predator detection and evasion, and lead the chicks to good foraging habitat, although the chicks forage for themselves (Warnock and Gill 1996).

Study Area

This study was conducted near Barrow, Alaska (71°18″N, 156°45″W), between early June and early August in 2008 and 2009. The low-lying tundra landscape is interspersed with ponds and lakes, and consists of a mosaic of low, wet marsh habitat and slightly higher, well-drained upland habitat (Brown et al. 1980). Dunlin nest primarily in upland habitat and lead chicks to wetter habitat after hatch (Holmes 1966b).

We investigated survival of chicks from three nest categories: 1) initial (i.e., first), un-manipulated nests, 2) early replacement nests, and 3) late replacement nests. The latter two categories were derived by experimentally removing entire clutches of initial nests in either early (3 – 8 days) or late (12 – 16 days) incubation. Initial, un-manipulated nests were located in or near six 0.36 km^2 plots in a study area situated to the east-southeast of Barrow (hereafter termed un-manipulated area; Fig. 2.1). Nests in the replacement categories were located in an area approximately 5 – 10 km west of these plots (hereafter termed experimental area; Fig. 2.1). Separate study areas were used for the un-manipulated and replacement nest categories to maintain the integrity of a long-term shorebird ecology study.

Potential predators of chicks included Pomarine (*Stercorarius pomarinus*), Parasitic (*S. parasiticus*), and Long-tailed (*S. longicaudus*) Jaegers; Glaucous Gulls (*Larus hyperboreus*); Snowy Owls (*Bubo scandiacus*); least (*Mustela nivalis*) and long-tailed (*M. frenata*) weasels; and arctic fox. Predator and lemming (an alternative prey) numbers were both high in 2008 and low in 2009 (Table 2.1). Predator and lemming

abundances within a year were similar across both the un-manipulated and experimental areas (B. L. Hill and R. B. Lanctot unpubl. data), and fox removal occurred throughout the entire study area in both years.

Field Methods

We searched for initial nests daily from early-June to mid-July using adult behavioral cues to locate nests, by flushing adults incidentally, or by systematically rope dragging the study area (see Naves et al. 2008 for methodology). We predicted hatch date by adding 21 days (incubation period for this species; Holmes 1966a) to the incubation start date. Nests found during laying were re-visited to determine final clutch size and the start of incubation. For nests found after clutch completion, the start of incubation was determined by floating eggs (Liebezeit et al. 2007). We checked nests every four days during the first 2.5 weeks of incubation, and daily near the estimated hatch date to ensure all chicks were marked. Eggs from initial nests in the experimental area were removed either 3 – 8, or 12 – 16, days into incubation to create early removal and late removal nest categories, respectively. Experimental nests were assigned to the early or late removal category using a systematic random design. There was no difference in initiation dates between the three nest categories (Gates 2011).

Adults were captured on the nest using a bow-net (Bub 1995), and were marked with a U.S. Geological Survey (USGS) metal leg band and a unique color band combination using Darvic® bands. We used morphological measurements to sex adults in the field (females are generally larger than males; Warnock and Gill 1996), and verified sex assignment later with genetic testing. To locate replacement nests and track broods, we placed radio transmitters on males and females in the experimental area, and on males only in the un-manipulated area (males typically care for the young). Females from un-manipulated nests were individually color-marked to enable monitoring for brood attendance. Transmitters (Model A2455, 1.2 g, Advanced Telemetry Systems, Isanti, Minnesota; or Model BD-2, 1.4 g, Holohil Systems Ltd., Ontario, Canada) were

attached by clipping feathers to the skin 1cm above the uropygial gland and then gluing the radio to the skin (Warnock and Warnock 1993).

We caught chicks by hand at or near the nest within 24 hours of hatch. Chicks were marked with a single USGS metal leg band which was covered with a thin piece of colored tape (black, blue, red, or white) for individual identification within a brood. To reduce the chance of potential complications (e.g., bands getting entangled in vegetation or attracting predators; but see Bart et al. 2001), we did not use Darvic® color band combinations on chicks. Chicks were weighed to the nearest 1.0 g using a 30 – 50 g spring scale in 2008 (Pesola®, Barr, Switzerland) and to the nearest 0.1 g with an electronic scale in 2009 (Ohaus®, Pine Brook, NJ). Two chicks from each brood were randomly selected to be radio-tagged. Transmitters (Model A2414, 0.3 g, Advanced Telemetry Systems, Isanti, Minnesota; or Model LB-2N, 0.35 g, Holohil Systems Ltd., Ontario, Canada) were attached using the same technique as for adults (Warnock and Warnock 1993). In addition, we glued surrounding down feathers over the top of the transmitter for camouflage and to increase retention (Whittier and Leslie 2005). The transmitters weighed 4.3% or 5.0% (depending on model) of the body mass of a typical 7.0 g chick. Chicks were kept warm during the marking process by placing them in a small cooler heated with chemical packs.

Chicks were monitored every other day until death or 15 days of age (hatch day = age 0, so 16 days total), which was the age we first saw chicks fly. Broods were located by first locating the radio transmitter signal of the attending adult because adult radios were larger and had a stronger signal and therefore could be heard from a farther distance than the chick radio transmitter signals. If the attending parent was not equipped with a radio (e.g., females from un-manipulated nests), we used chick radio transmitter signals to locate the brood. After visually locating the attending adult we retreated until it stopped alarm calling and resumed contact calling with its chicks (similar to "gather call" in Johnson et al. 2008). This distance typically varied from 20 – 40 m, depending on the individual adult and age of the chicks. We then located the chicks using their radio

transmitter signals and with visual observations. We conducted a 5-min observation of the brood to visually determine the number and identity of chicks (when possible), to identify adults, and to record whether or not an adult exhibited brood-rearing (hereafter referred to as broody) behavior. Broody adults sounded alarm calls or performed a "rodent run" distraction display (Brown 1962) when an observer approached the brood, then initiated contact calling with chicks when the perception of "danger" abated. Non-broody adult behavior included foraging rapidly, preening diligently, roosting, and allowing observers to approach without alarm calling. If a chick was not observed visually but the radio signal was loud and in the direction of the parent, we considered the chick to be alive. If the radio signal was weak or was not in the direction of the parent, we attempted to locate the chick. If a chick radio signal was not heard, we listened for it in the surrounding area. We checked for missing chick radio signals for the remainder of the season to maximize the possibility of relocating a chick that was alive but separated from its brood, or a chick that had died.

Chicks were classified as alive if visually observed, if a strong radio signal was detected near the adult, or, in the case of a missing chick radio signal, if the attending adult demonstrated broody behavior. Chicks were classified as dead if a carcass was found, if their radio signal was missing and the attending adult did not exhibit broody behavior for two consecutive visits, or if the radio signals for both the adult and chick were missing for the remainder of the season. For retrieved carcasses, we assigned cause of death using the following criteria: chicks found intact on the surface of the tundra with no apparent flesh wounds were presumed to have died of exposure; chicks found in burrows with gashes or bite marks were presumed to be depredated by weasels; and chicks whose radio was found in a pellet were presumed to be depredated by an avian predator. We note that it was not possible to determine whether a chick died from exposure before being depredated. We continued to monitor broods that stayed in the study area for > 16 days to determine how long they were attended by a parent. An aerial

telemetry flight was conducted in late July 2009 in an attempt to locate missing adults and chicks.

We used pitfall traps to estimate insect biomass during the chick-rearing period following the protocol in Tulp and Schekkerman (2008). One transect, with ten traps spaced 20 m apart – five in mesic habitat and five in xeric habitat – was established in each of the experimental and un-manipulated study areas (Fig. 2.1). Traps were constructed of a 16 oz clear plastic drinking cup that was cut to approximately 9 cm in height, resulting in an 8 cm diameter opening. Traps contained approximately 2 cm of water and a few drops of laundry detergent (to reduce surface tension and prevent insects from escaping), and were placed into the tundra so that the rim was flush with the ground. We collected all insects from the traps every other day between 23 June and 6 August. Insect lengths were measured to the nearest 0.5 mm when their total length was less than 5.0 mm and to the nearest 1.0 mm when their total length was more than 5.0 mm (Tulp and Schekkerman 2008). Adult and larval insects were identified to order, and length was converted to a dry mass weight (mg) using regression models developed for Araneida, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (and their larvae) by Rogers et al. (1977). Total dry mass of insects per 2-day period was calculated as the average of the total dry weight over the two study areas. The average 2-day total dry mass of the two adjacent days was used to calculate a 2-day total dry mass for days between sampling occasions.

We acquired average daily air temperatures from the Wiley Post-Will Rogers Memorial Airport in Barrow, which was located between 2 and 10.5 km from chick-rearing areas (http://www.weather.gov/). There was continuous daylight throughout the entire study period.

Data Analysis

Chick survival – We used nest survival models in program MARK (Version 6.1) to estimate chick daily survival rates (DSR; Rotella et al. 2004). Nest survival models are

a type of known fate model (i.e., detection probability is not estimated), which allow staggered observations and an unknown day of death (Dinsmore et al. 2002). Nest survival models assume that: 1) chicks are correctly aged on the first visit, (2) fates are known with certainty, (3) brood checks do not influence survival, (4) chicks are independent, and (5) survival among chicks is homogeneous (Dinsmore et al. 2002). We are confident that assumption 1 was met because we checked nests daily near the expected hatch date, and chicks were banded in the nest bowl or close by. Assumption 2 may not have been met in all cases as not all fates (alive or dead) were known with certainty. We attempted to minimize error in assigning fates based on a combination of indicators: presence of a carcass, adult behavior, and presence/absence of a radio signal. We expect assumption 3 to be met because brood checks were conducted at a distance that appeared not to cause disturbance (i.e., after contact calling resumed chicks performed normal behaviors). Some violation of assumption 4 likely occurred, especially in the first few days after hatching, because we monitored two chicks from each brood. However, chick behavior suggests chicks from the same brood act more independently of each other as they get older (e.g., distance between brood-mates increases; B. L. Hill pers. obs.). Finally, it is likely that there is at least some non-homogeneity in chick survival, a violation of assumption 5. We attempted to account for some of this potential variability by including models with individual covariates for factors expected to cause differences in survival among individuals. Unfortunately, there is currently no unbiased technique for estimating extra-binomial variation (lack of independence and homogeneity) in nest survival models (Dinsmore et al. 2002), but we discuss the use of the variance inflation factor ($\hat{c}$) to address this below.

We used an information-theoretic approach (Burnham and Anderson 2002) for model development and selection. We developed a set of *a priori* models based on five variables observed to influence chick survival in prior studies: insect biomass (I), air temperature (T), year (Y), chick age as a linear (A) or quadratic ($A + A^2$) function, and hatch date as a linear (HD) or quadratic ($HD + HD^2$) function. We used hatch date rather

than a categorical variable of the three nest categories to maximize the use of information in the data and to avoid error from misclassification of initial and replacement nests, which overlapped for a short period. Insect biomass and daily average air temperature were not correlated for our data set (r^2 = 0.016 for 2008; r^2 = 0.092 for 2009). Our model set included all combinations of single, two and three variable models with additive and/or interactive effects, with the following exceptions: 1) an interactive effect of year and insect biomass was not considered, as we assumed insect biomass would have the same effect on chicks regardless of year; 2) temperature was only considered as an interactive effect with chick age, as we assumed young chicks were disproportionately affected by cold temperatures; and 3) we did not consider models including 3-way interactions. We did not consider models with > 3 factors to avoid over-fitting the data. The model set included 75 models.

We determined model rankings using AIC adjusted to account for sample size (AIC_c) and for overdispersion of the data ($QAIC_c$). We used $\hat{c}$ (estimated as model deviance divided by the degrees of freedom) from our most parameterized model to re-scale our AIC values to quasi-likelihood values and to inflate variance estimates (Burnham and Anderson 2002). This method for estimating $\hat{c}$ is likely an overestimate and therefore made our conclusions conservative. We are confident this adequately accounts for any lack of independence of fates in our data. Models with $\Delta QAIC_c < 2.0$ were considered best to explain the data, and variables within models were considered important if 85% confidence intervals for the beta estimates did not overlap zero. We determined variable support by summing model weights of all models with that variable and then rescaling those values so that the summed weight for the most supported variable was 1.0. We back-transformed DSR from logit to real scale. The probability a chick survived from hatching to 15 days of age was calculated as

$$\hat{S}_i = DSR_{i,j,0}DSR_{i,j,1}DSR_{i,j,2}\ldots DSR_{i,j,15}$$

where i is hatch day, j is insect biomass, and subscripts 0 – 15 are chick age. We used the delta method to estimate variances (Seber 1982).

Deserting adult attendance – In Dunlin, one adult of a pair typically leaves the brood soon after hatching and the remaining adult (typically the male) assumes the brood-rearing role (Warnock and Gill 1996). We hereafter refer to the former as the deserting adult. To evaluate whether the length of time deserting adults stayed with the brood was related to hatch date, we conducted a linear regression analysis of the number of days between chick hatching and brood desertion relative to hatch date.

RESULTS

Chick Monitoring

The earliest and latest dates chicks hatched were 25 June and 24 July, respectively. The chick-rearing period, from the earliest date chicks hatched until the latest date chicks were monitored (6 August), was 43 days. Chicks from initial nests generally hatched between late June and mid-July, whereas chicks from early and late replacement nests hatched around mid- and late-July, respectively (Fig. 2.2). We radio-tagged 2 chicks from each of 66 broods (n = 38 in 2008; n = 28 in 2009). We excluded one chick from further analysis because it failed to leave the nest bowl and its death was attributed to handling and marking. In 2008, sample sizes were 19, 13, and six broods for initial, early replacement, and late replacement nests respectively. In 2009, 20, seven, and one nests were from initial, early replacement and late replacement nests, respectively. Despite target sample sizes of 20 for each nest category, replacement nest sample sizes were lower than initial nest sample sizes because not all pairs re-nested and some replacement nests were depredated before the chicks hatched.

Of the 66 broods, both radio-tagged chicks survived to 15 days of age in 29 broods, only one radio-tagged chick survived to 15 days of age in three broods, and no radio-tagged chicks survived in the remaining broods. Fifty-three percent and 75% of initial broods had at least one chick survive to 15 days of age in 2008 and 2009, respectively. In contrast, only 21% and 38% of replacement broods had at least one chick survive to 15 days of age in 2008 and 2009, respectively. Of the 34 broods that

experienced total brood loss, 21 broods had both chicks die during the same 2-day sampling period, while the remaining broods had one chick live for at least one additional day (average time between deaths = 5.25 ± 0.94 SE days, range: 1 – 10). Chicks died at a wide range of ages, from 1 to 14 days of age (Fig. 2.3), and across the chick-rearing period (Fig. 2.4). Of the 70 chicks classified as dead, 59% were never found, 24% apparently died from exposure, 10% were depredated by weasels, 1% by an avian predator, and in the remaining 6%, cause of death could not be inferred from the carcass. Most exposure deaths occurred on days following low temperatures and low insect biomass (Fig. 2.4).

Environmental Variables

Insect biomass peaked in early July in both years, after which it generally declined. Biomass varied between 0.00 – 499.02 mg/2-days in 2008 and 44.57 – 733.40 mg/2-days in 2009 (Fig. 2.4). The most common insects sampled were Diptera and Araneida, comprising 58.3% and 33.6% of the total capture, respectively. The remaining orders made up < 4.0% each. Daily average temperatures were 4.2° C (range: 0.0 to 10.0° C) in 2008 and 6.3° C (range: -0.6 to 13.9° C) in 2009 (Fig. 2.4).

Chick Survival

Goodness-of-fit and model selection – The estimated $\hat{c}$ values for our two most general models were 3.08 (model $I + HD + HD^2 + A + A^2 + HD*A + HD*A^2 + HD^2*A + HD^2*A^2$) and 3.14 (model $Y + HD + HD^2 + A + A^2 + HD*A + HD*A^2 + HD^2*A + HD^2*A^2$). We used the highest of these two values, $\hat{c} = 3.14$, to calculate AIC_c values and inflate sampling variances. Seven models had $\Delta QAIC_c$ values < 2.0, and an additional 18 models had $\Delta QAIC_c$ values < 4.0 (Table 2.2). The top seven models included hatch date, insect biomass, and chick age as explanatory variables. Each of these variables had summed model weights > 0.88 (Fig. 2.5). In contrast, year and temperature had summed model weights of only 0.34 and 0.03, respectively, and were not included in the top

models. We report DSR estimates from the top model rather than model-averaged DSR estimates of the top seven models because these were within 5% of the model-averaged estimates, except for a few cases (at very low insect biomass and very late hatch dates), and because parameters could not be averaged across these models, as they included interaction and quadratic terms (Burnham and Anderson 2002). The top model estimating DSR (on the logit scale) was (SE in parentheses): logit(DSR) = -0.278 (2.109) + 0.005 I (0.003) + 0.177 HD (0.108) + 1.010 A (0.516) – 0.061 A^2 (0.031) – 0.085 HD*A (0.033) + 0.006 HD*A^2 (0.002). None of the 85% confidence intervals for the beta coefficients overlapped zero, all variables were well supported (Fig. 2.5), and model deviance is lowest in this top model, suggesting no uninformative parameters are present. Calculating DSR for the top model required a single daily value for insect biomass, so we averaged insect biomass over 2008 and 2009 for each day of the season, then smoothed the average values using the lowess method (smoothing parameter = 0.25; Cleveland 1979).

DSR relationships – DSR increased with increases in insect biomass and hatch date (for most conditions), but showed a more complicated relationship with chick age as a result of the interaction and quadratic terms in the model. DSR declined with decreasing insect biomass, with the greatest declines occurring for late hatch dates (Fig. 2.6). In most cases DSR declined with hatch date, although this pattern was reversed for the youngest and oldest chicks when insect biomass was low (Fig. 2.7). Our data showed contrasting patterns of DSR with chick age for early and late hatching chicks (Fig. 2.7). DSR was high and relatively stable across chick ages and insect biomass for early hatching chicks (e.g., 3 July). As hatch date increased, DSR showed an increase with chick age for chicks up to about one week old, then roughly leveled off. For late hatching chicks this transitioned to a relationship where DSR was lowest when chicks were about one week old, and was relatively high for young and old chicks. These patterns were very slight when insect biomass was high and much more pronounced when insect biomass was low.

Probability of surviving to 15 days of age – We calculated the probability a chick survived to 15 days of age using DSR estimates from the top model. The probability that a chick survived to 15 days of age was above 0.50 for chicks hatching in late June or the first week of July, peaking around 0.73 on 1 July (Fig. 2.8). This probability declined rapidly for chicks hatching in the second week of July (from approximately 0.55 to 0.20) and was very low (< 0.20) for chicks hatching after mid-July. The probability a chick survived to 15 days of age was dramatically higher for the average hatch date of initial nests, 0.71 ± 0.07, than for the average hatch date of early or late replacement nests, 0.23 ± 0.19 and 0.03 ± 0.61, respectively. However, standard errors for very early or late hatching chicks were large because of low samples sizes. The latest hatch date for which we could calculate the probability of a chick surviving to 15 days of age was 22 July, because we could only estimate DSR through 6 August, 15 days from that date. By weighting the probability of a chick surviving to 15 days of age for each hatch date by the number of chicks that hatched on that day, we estimated the overall probability that a chick survived to 15 days of age as 0.481 ± 0.004 SE.

Deserting adult attendance patterns – All but one of 66 broods were attended by at least one parent until the chicks died or at least one chick survived 16 days. In the brood where both parents deserted, one chick survived at least 16 days, although the female and male had deserted at six and eight days, respectively. In six broods, both parents remained until the brood died (between 1 and 10 days), and in four broods, the second parent was not color-marked and thus we could not determine its attendance time. These 10 broods were not included in the following analysis. The average attendance time of the deserting adult was 3.18 ± 0.45 (range: 1 – 11, n = 33), 1.59 ± 0.48 (range: 1 – 9, n = 17), and 1.71 ± 0.47 (range: 1 – 4, n = 7) for initial, early replacement, and late replacement broods, respectively. In 42%, 88%, and 71% of initial, early, and late replacement broods, respectively, the deserting adult stayed only one day (Fig. 2.9). Females typically deserted before the male (50 of 56 broods). The number of days the deserting adult attended the brood before leaving decreased as hatch date increased: β = -

0.10 ± 0.04 SE (Fig. 2.10). The number of days before desertion for females from initial nests is potentially negatively biased because these birds were not radio-tagged, and were therefore more difficult to detect. This would weaken the relationship between the number of days before desertion and hatch date. Removing broods for which both adults were still attending when brood failure occurred from the analysis could also negatively bias the number of days attending because the time of brood failure represents the earliest possible desertion date. This could strengthen or weaken the relationship between the number of days attending and hatch date depending on the distribution of hatch dates for these broods and when brood loss occurred.

DISCUSSION

Chicks that hatched early in the season had a much better chance of surviving to 15 days of age than chicks hatching later in the season: a 2 in 3 chance for chicks from broods hatching from initial (first) nests compared to a 1 in 4 chance for chicks from broods hatching from early replacement nests. Our results suggest the chance of surviving to 15 days of age for chicks hatching from late replacement nests is even lower, but we advocate caution in making inference from these values because of their large standard errors. Jamieson (2011) saw a similar decline in the number of nests that produced at least one fledgling from replacement nests (37%, n = 19) when compared to first nests (74%, n = 53) of Dunlin in sub-arctic Alaska. Similarly, Soikkeli (1967) determined that 87 – 89% of Dunlin nests in Finland fledged at least one chick if they hatched before 10 June, whereas only 20% fledged at least one chick if they hatched later. In contrast, Jönsson (1991) found that first-year birds from early- or late-hatching broods had similar first-year return rates, suggesting that chicks from later-hatching nests fared as well as earlier-hatching chicks.

Our estimate of the probability of a chick surviving to 15 days of age for all nests (0.48) is within the range of values described elsewhere. Reported estimates of Dunlin chick survival to fledging in Scandinavia cover a wide range of values: 34% for estimates

based on first-year return rates (Jönsson 1991), 31-60% based on post-breeding fledgling counts (Blomqvist and Johansson 1991), and 64% based on chicks recovered after fledging (Casén and Hildén, in Soikkeli 1967). For other small Arctic shorebird species, chick survival to fledging has been reported as 26% for Buff-breasted Sandpiper (*Tryngites subruficollis*; Lanctot 1994), 45% for Ringed Plover (*Charadrius hiaticula*; Pienkowski 1984), 43% for Curlew Sandpiper in Russia (*Calidris ferruginea*; Schekkerman et al. 1998), and Ruthrauff and McCaffery (2005) determined that the overall probability of a chick surviving to fledge was 0.73 ± 0.05 SE for Western Sandpipers (*Calidris mauri*) in subarctic Alaska. Further comparisons of our estimates with other studies is limited by differences in field and analytic methodology, differences in the length of time for which estimates were calculated, and the lack of information on the temporal and spatial variability of these parameters. But we note that the estimates generated by our study may be inflated, at least in part, as a result of reduced predation and increased DSR resulting from fox removal. Further analysis would be needed to evaluate the degree to which fox removal influences survival rates.

Factors Important to DSR of Dunlin Chicks

DSR was generally negatively associated with hatch date, positively associated with insect biomass, and showed both positive and negative associations with chick age. These relationships were weak for early hatch dates and when insect biomass was high, becoming pronounced only for late hatch dates and low insect biomass.

Hatch date – In our study, under most conditions, chicks hatching earlier in the season had higher survival probabilities than chicks hatching later in the season – up to a ten-fold difference when insect biomass was low. A seasonal decline in chick survival has also been observed in other shorebird studies (Soikkeli 1967, Ruthrauff and McCaffery 2005, Tulp 2007, Hartman and Oring 2009). In studies of other avian taxa, a seasonal decline in chick survival has been variously attributed to decreasing food availability (Daan et al. 1989, Lepage et al. 1998), increasing food requirements of

predators (Naef-Daenzer et al. 2001, Sunde 2005), or parental care restraints (e.g., less experienced or lower quality parents breeding later [Perrins 1970] or abandoning young [e.g., Ruthrauff et al. 2009]). We discuss food (see *Insect biomass*) and predators (see *Year*) later.

In terms of parental quality, there was no difference in the initiation date of un-manipulated nests and initial nests assigned to a replacement treatment (Gates 2011) – all of which were initiated early in the season. So we have no reason to believe that adults that laid replacement nests were unfit or of low quality. Unfortunately, our data did not allow us to assess the effect of brood desertion on chick survival in our modeling. However, in line with other studies, we found that the length of time a deserting adult stayed with the brood decreased across the season (Currie et al. 2001, Ruthrauff et al. 2009). But contrary to other studies (Neville 2002, Ruthrauff et al. 2009), we found that chicks rarely suffered total abandonment, and the only instance where both adults deserted their chicks while they were still alive was from an initial (un-manipulated) nest. In addition, non-deserting adults stayed with their broods for 21 days, on average (B. L. Hill unpubl. data), in both initial and early replacement broods, suggesting that Dunlin may not be under a time constraint in our study area, which might otherwise cause them to abandon their young.

Insect biomass – We found that chick DSR was related to insect biomass, and as would be expected, chicks that hatched just before the peak insect emergence, thus experiencing the highest insect availability, had higher probabilities of surviving to 15 days of age. These relationships are supported by other studies that have shown that young hatching before the peak in food abundance have higher growth rates (Daan et al. 1989, Lepage et al. 1998, Schekkerman et al. 2003) – which in turn has a positive effect on survival (Kersten and Brenninkmeijer 1995, Schekkerman et al. 1998, Starck and Ricklefs 1998, Pearce-Higgins and Yalden 2004, Tulp 2007) – and studies that have shown a positive relationship between survival rate and insect availability (Schekkerman et al. 2003, Tulp 2007). Chicks hatching late in the season experienced prolonged periods

of, or in some cases only experienced, conditions of low insect biomass, which could reduce survival through a number of paths, including: reduced growth rate, increased energy requirements for foraging and thermoregulation, reduced vigilance as a result of increased time spent foraging, or poorer condition (e.g., Tulp and Schekkerman 2001, Schekkerman et al. 2003). Indeed, deaths attributed to exposure occurred when insect biomass was very low (Fig. 2.4).

Chick age – In many studies, researchers report that newly hatched chicks have the lowest survival (Soikkeli 1967, Schekkerman et al. 1998, Pearce-Higgins and Yalden 2002, Ruthrauff and McCaffery 2005). Reasons cited for this include the inability of young chicks to thermoregulate and forage efficiently, as well as their susceptibility to predation. In contrast, although we showed this pattern for chicks with an early hatch date, chicks hatching later had the lowest survival at 7 days of age. The lack of fox in our study area may have artificially increased survival of the youngest chicks. Adults are typically more obvious at this time, exhibiting distraction displays and alarm calling, which can bring in other adult Dunlin (Soikkeli 1967, B. L. Hill pers. obs.) or adults of other species (Jehl 1973), thereby likely increasing the likelihood of a predator finding the brood. Chicks are also very near one another at this time, which would increase the chance of total brood loss if found (Safriel 1975). High survival of young chicks due to the lack of fox could have meant that chicks were then at a greater risk of dying around age 7 days due to their susceptibility to poor food and weather conditions. Yolk reserves are used up during the first few days after hatch (Nice 1962, Norton 1973) so chicks must rely solely on external food sources and therefore are more vulnerable to periods of low food availability (see *Insect biomass*), which chicks hatching later in the season are more likely to experience. Also, as chicks mature, they need and receive less brooding (Norton 1973, Ashkenazie and Safriel 1979, Krijgsveld et al. 2003, Schekkerman and Boele 2009). However, Norton (1973) observed that chicks as old as 8 days of age would emit distress calls and act sluggish if their core temperature dropped below 30°C, indicating they are still vulnerable to cold temperatures at that age. If both parents are present, they

can both brood chicks, which likely is important at older ages, as four chicks can no longer fit under one adult. We found that both parents were less likely to be present around 7 days of age for later hatching chicks. Additional study is needed to validate whether newly hatched young are more easily detected by predators, but this is certainly the case for humans locating broods (Safriel 1975, Lanctot et al. 1995, this study).

Further study is also required to determine if chicks from replacement nests come from lower quality eggs (i.e., the female puts less resources into replacement nest clutches compared to first clutches). Incidental captures of chicks from initial and replacement nests indicated that chicks from replacement nests had slower growth rates and were not able to fly until they were much older (chicks as old as 26 days would not fly when approached). For example, chicks from initial and early replacement nests, hatching no more than four days apart, had dramatic differences in wing development at 16 and 17 days of age despite experiencing similar environmental conditions (Fig. 2.11). Although evidence is purely anecdotal, this suggests these differences may be the result of lower egg quality (e.g., composition) between initial and replacement clutches (e.g., Nager et al. 2000). If so, this could mean that initial and replacement chicks are developing at different rates and thus are likely to differ in food and brooding requirements across age.

Year – We were surprised that year was not an important explanatory variable in our analysis, as the two years of our study were very different, especially in terms of predator and prey abundances (Table 2.1). Under the alternative prey-switching hypothesis (Roselaar 1979, Summers 1986), we would predict higher rates of mortality in 2009 than 2008, when predators should have switched to feeding on bird eggs and chicks due to the low number of lemmings in the area. However, we observed a greater number of chick deaths in 2008 than 2009. Our results were even more surprising given that hatching success was much higher in 2008 (76%) than 2009 (32%; R. B. Lanctot unpubl. data), which is consistent with the prey-switching hypothesis. This hypothesis has been supported in many other studies on shorebirds, arctic-breeding geese, and arctic fox

(Summers and Underhill 1987, Underhill et al. 1993, Summers et al. 1998, Strand et al. 1999, Bêty et al. 2001, Blomqvist et al. 2002, McKinnon and Bêty 2009), although Soloviev et al. (2006) and Liebezeit and Zack (2009) failed to see lower chick or nest survival when small mammal numbers were low. We believe that high lemming numbers in 2008 led to an influx of avian and small mammal predators (that were not present in 2009), which subsequently resulted in higher predation on chicks.

Temperature – Temperature had very low support in our analysis. This result is surprising given that two cold spells late in July of 2008 killed many replacement nest chicks, while a similar cold period earlier in the month did not result in the deaths of any chicks from initial nests (although food was more abundant early on; Fig. 2.4). Adverse weather conditions have been shown to have a negative effect on the survival of arctic shorebird chicks (Meltofte et al. 2007, Tulp 2007). In periods of inclement weather, chicks are brooded more frequently, leaving less time for foraging (Beintema and Visser 1989, Tjørve et al. 2007). Not surprisingly, slower growth rates have also been observed during poor weather (Schekkerman et al. 1998, Tjørve et al. 2007), which can lead to an increase in the length of the pre-fledging period, which likely leads to lower survival rates. Indeed, Beale et al. (2006) found that recruitment of Dunlin was higher after summers of warmer weather, and Soloviev et al. (2006) reported a significant decrease in juveniles of four arctic-breeding shorebird species with decreases in July temperatures on the breeding grounds in Siberia. Temperature may not have been important in our study because of a similar relationship with day of season and a smaller effect on survival than insect biomass.

Study Limitations

Two assumptions in our survival analysis may not have been met. First, we may have mis-categorized missing chicks as dead or dead chicks as alive. Missing chicks could have been alive but abandoned by their parent, adopted by another brood, or simply not seen or heard during observations. Concluding a chick was dead would have been

reinforced if the parent(s) began acting non-broody. We found little evidence to suggest this occurred. We could find chicks that were not observed or not with their brood using their radio transmitters, and only two chicks were known to join another brood, which in both cases was a temporary stay. In one case, a 2-day-old chick was observed with another brood at a common brood-rearing site, but was back with its parents two days later. The parents continued to act broody and tend their other chicks during this time. In the second case, a 19-day-old chick was found with another brood, and then observed alone at 21 days of age (this was the chick where both parents abandoned their brood). However, three chick radios were heard from the telemetry flight approximately 2 – 3 km from the last site they were recorded as alive and were not re-located on the ground. We assumed these three chicks had died, either because their parent's signal was not near them and the parent was not broody for two consecutive visits before the flight, or because the adult was missing and its radio signal was not heard on the telemetry flight, suggesting the parent had moved out of the study area and was no longer caring for their chicks. Although these chicks could have been alive and independent we feel this is unlikely. Overestimation of chick survival could have occurred if a missing chick was classified as alive, based on the behavior of a broody parent, but was actually dead. Although we did have 12 broods where date of death was different between brood-mates, we only had three broods where one radio-tagged chick survived to 15 days of age and the other chick died. So while we may have overestimated the length of time a chick was alive, the final fate was likely correct. In all cases where both radio-tagged chicks were dead the adult was not broody, suggesting that assigning a missing chick's fate based on adult behavior was reasonably reliable.

A second assumption that may not have been met is non-independence of brood-mates. We feel that adjusting results based on our high $\hat{c}$ more than compensated for this. In addition, our observation data suggests that chicks were relatively independent of each other. We found that not all broods suffered total brood loss on the same day (see above). Of these 12 broods, chick deaths were separated by 5 days on average, but as much as ten

days, indicating that chicks may be more independent of their brood mates than one might expect. Further, behavioral observations and radio detections revealed that chicks occupied a larger "brood" area as they matured, indicating that independence among chicks increases as chicks age – a pattern that has also been observed in congeners (Safriel 1975, Ruthrauff and McCaffery 2005).

Conclusions

We began this study by asking the question: "Does chick survival vary between initial and replacement nests?" The answer is emphatically "yes". Chicks hatching later in the season had lower survival, particularly when food conditions were poor. Our results seem robust across years given we had two very different years with opposite predator and lemming conditions. In addition, our survival estimates for replacement chicks may be inflated because their pre-fledgling period appears to be longer than that of initial chicks. Despite this apparent handicap experienced by later hatching chicks, Dunlin are known to stage at nearby river deltas on the North Slope through August (Taylor et al. 2011), providing an additional month or more for them to fully develop and prepare for the southbound migration. Further study of post-fledgling survival is needed to evaluate if replacement chicks have adequate time to acquire the resources necessary to survive their first trip south.

The poor survival of chicks from both early (0.23 ± 0.19) and late (0.03 ± 0.61) replacement nests, compared to initial (0.71 ± 0.07) nests, indicate that these nests should not be considered equal in terms of their contribution in productivity estimates. However, most researchers investigating nest success are unable to differentiate between initial and replacement nests (see Naves et al. 2008). Our study suggests that researchers, at a minimum, should consider hatch date as an important covariate in chick survival analyses, and weight later-hatching nests lower when estimating productivity.

This study provided valuable demographic information that will help inform investigations of the factors that influence population trends of *arcticola* Dunlin.

Information on other parameters such as survival of first-year birds are still needed to allow demographic modeling and assessment of the relative importance of different factors limiting population growth in Dunlin. We advocate exercising caution in interpreting the absolute value of our survival rate estimates and acknowledging the possible role of fox removal in inflating our estimates over what might be observed in other arctic regions. Investigation of chick survival in an arctic area where fox are present would be beneficial to assessing the degree of influence of foxes on chick survival.

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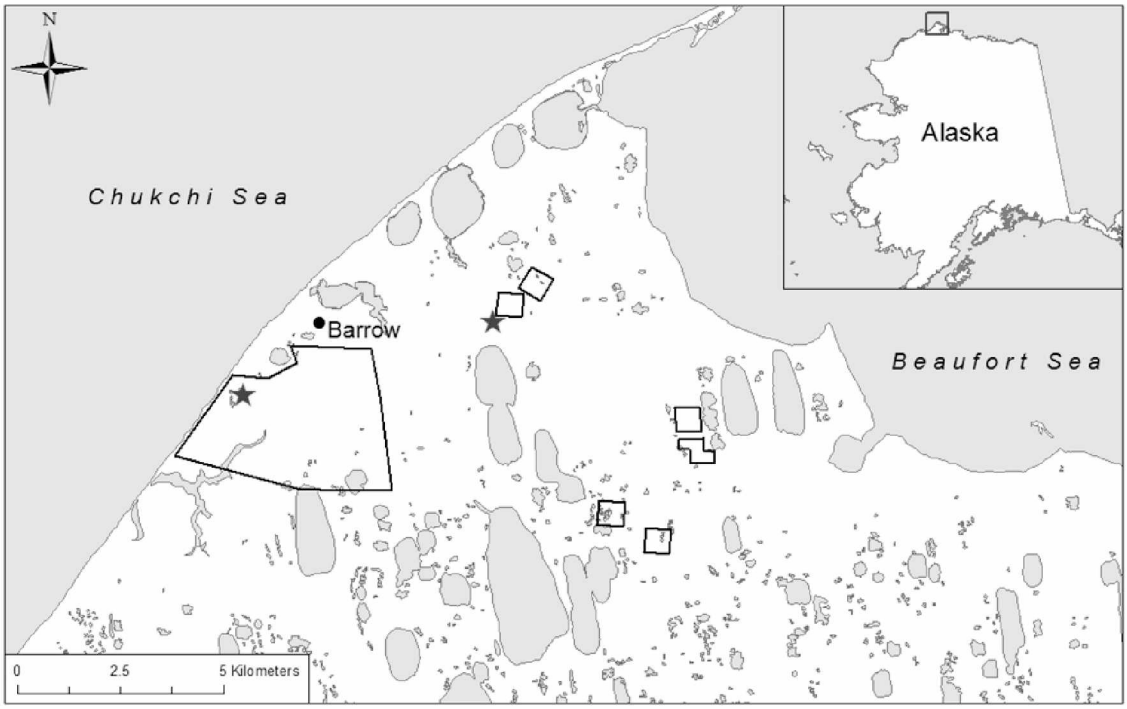

Figure 2.1. Locations of the six 0.36 km^2 plots making up the "un-manipulated" area (east of Barrow) and the approximately 10 km^2 "experimental" area (south of Barrow). Dunlin nests were located within or very near these study areas, however, broods frequently moved outside of them. Stars represent where insect traps were located. The filled circle marks the Wiley Post-Will Rogers Memorial Airport located in Barrow where daily temperature data were collected. The land illustrated in this figure (white) approximates the area searched for snowy owl nests and fox dens by other researchers. Fox removal took place throughout this entire area during both years of the study.

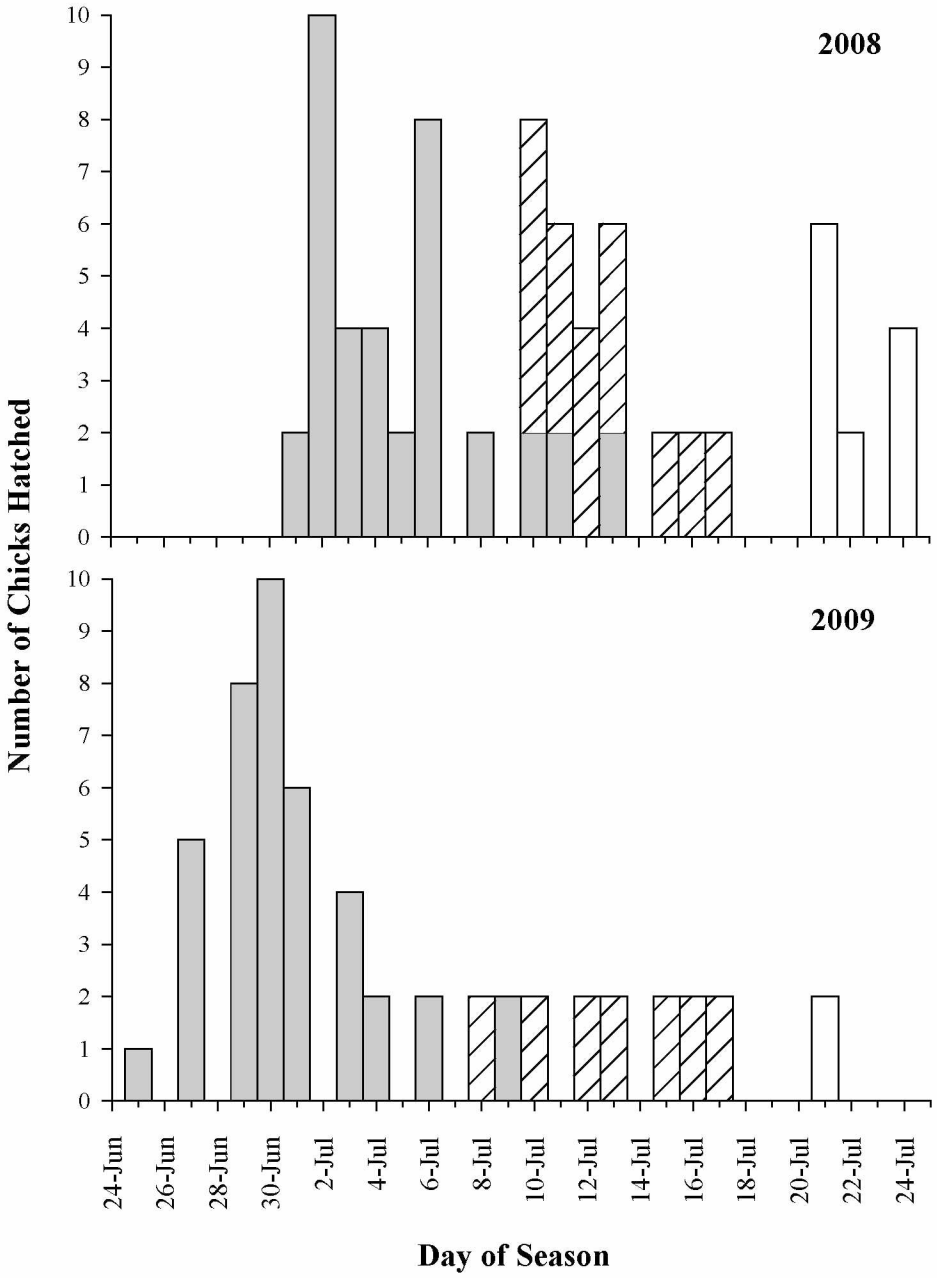

Figure 2.2. Hatch dates for 131 Dunlin chicks from initial (gray), early replacement (diagonal), and late replacement (white) nests in 2008 (n = 75) and 2009 (n = 56). Bars are stacked, e.g., two initial and six early replacement nests hatched on 10 July 2008.

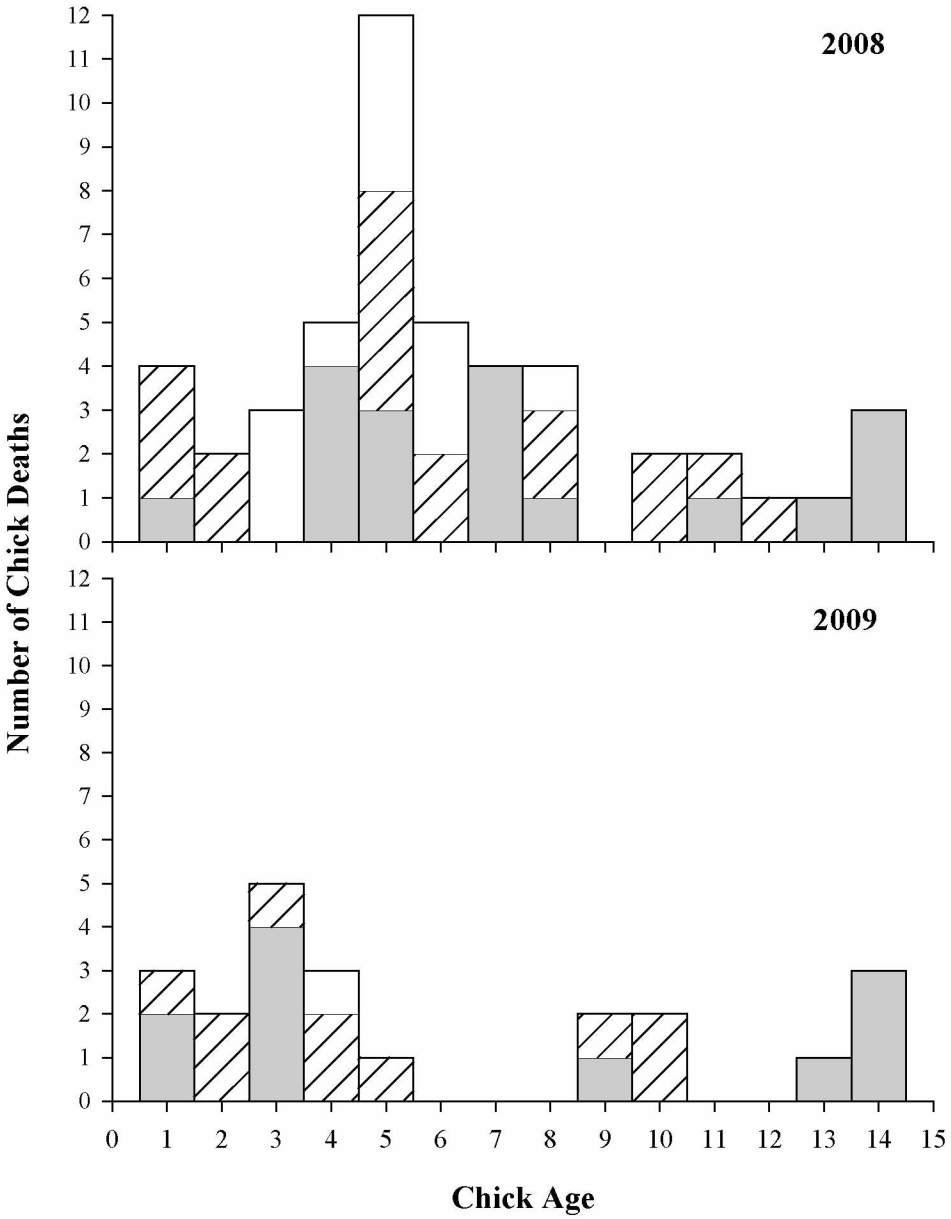

Figure 2.3. Age at death of Dunlin chicks from initial (gray), early replacement (diagonal), and late replacement (white) nests in 2008 (n = 48) and 2009 (n = 22). Because chicks were monitored every other day, age of death was calculated as age of chick on day between last known alive and day determined to be dead. Bars are stacked, e.g., one initial and three early replacement chicks died at age 1 in 2008.

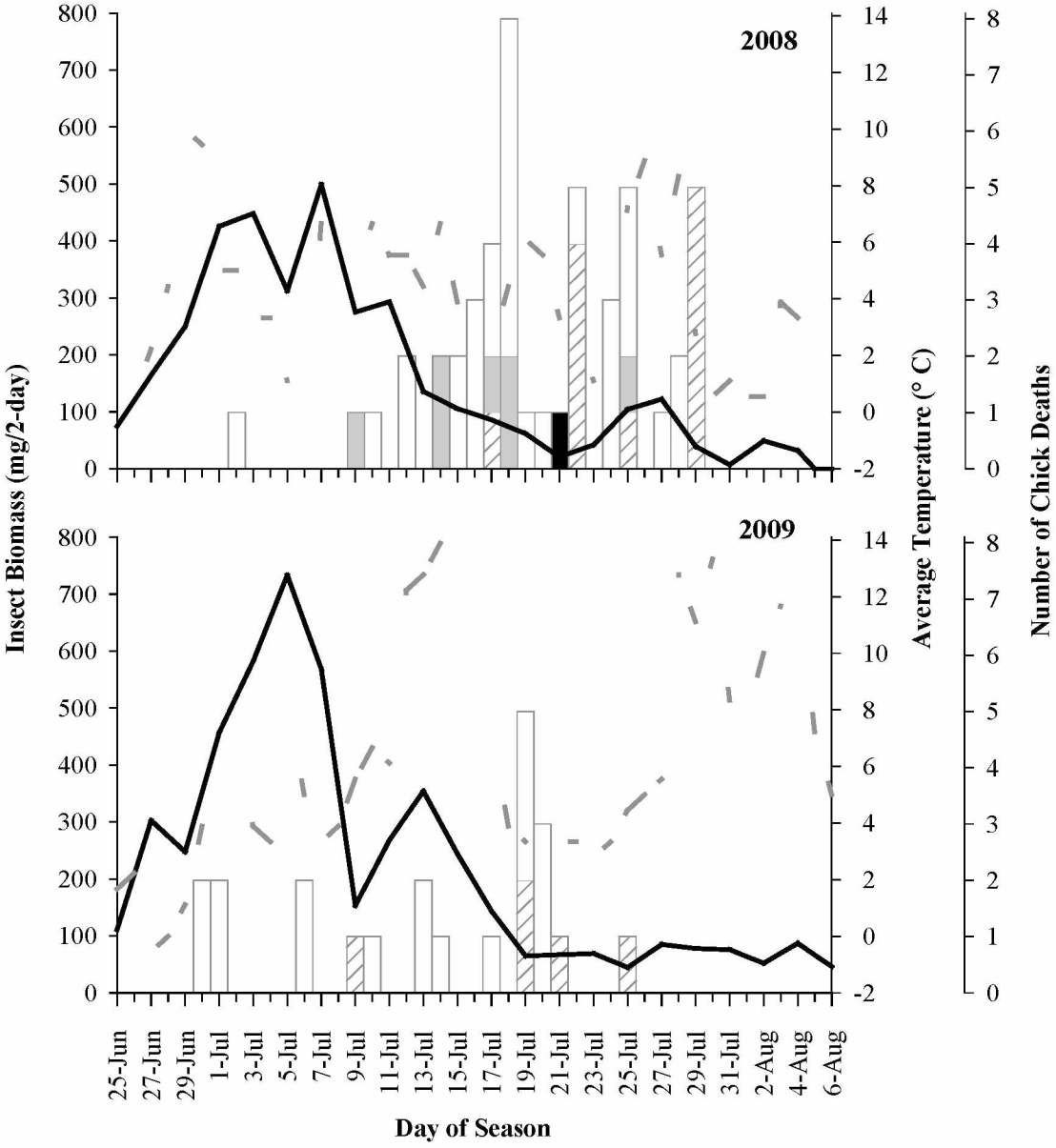

Figure 2.4. Estimated insect biomass (dry weight; solid line), average temperatures (dashed line), and number of chick deaths per day attributed to exposure (diagonal), weasels (light gray), avian predators (black), and deaths from unknown causes (i.e., chick was not recovered or death could not be inferred from carcass; white) in 2008 and 2009. Deaths are stacked, e.g., 2 deaths from exposure and 3 unknown deaths on 19 July 2009.

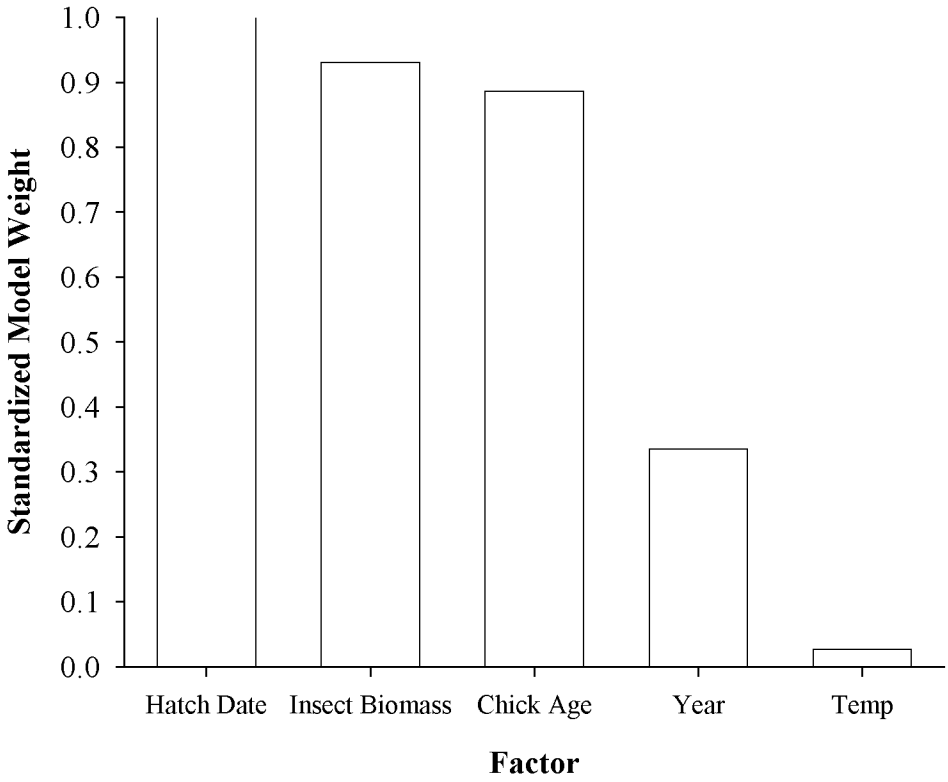

Figure 2.5. Summed model weights for explanatory variables in models estimating daily survival rates of Dunlin chicks. Results are re-scaled so the summed model weight for the variable with the most support is 1.0. Summed model weights include all models in the set (n = 75).

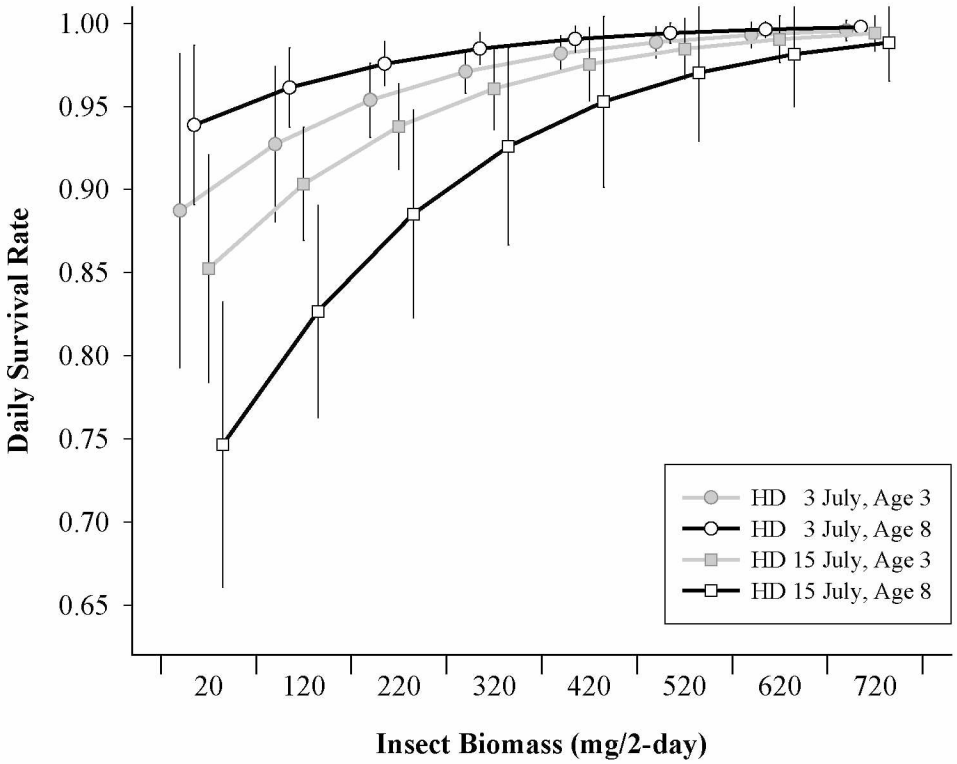

Figure 2.6. Estimated daily survival rates (± 1 SE) of Dunlin chicks as a function of insect biomass (dry weight; I), age (A), and hatch date (HD) from the top model ($I + HD + A + A^2 + HD*A + HD*A^2$). Estimates are presented for average hatch dates for initial nests (3 July) and early and late replacement nests combined (15 July), and for young and middle chick ages. The same insect biomass at symbol locations is used for each combination of hatch date and age but lines are offset so SEs are visible.

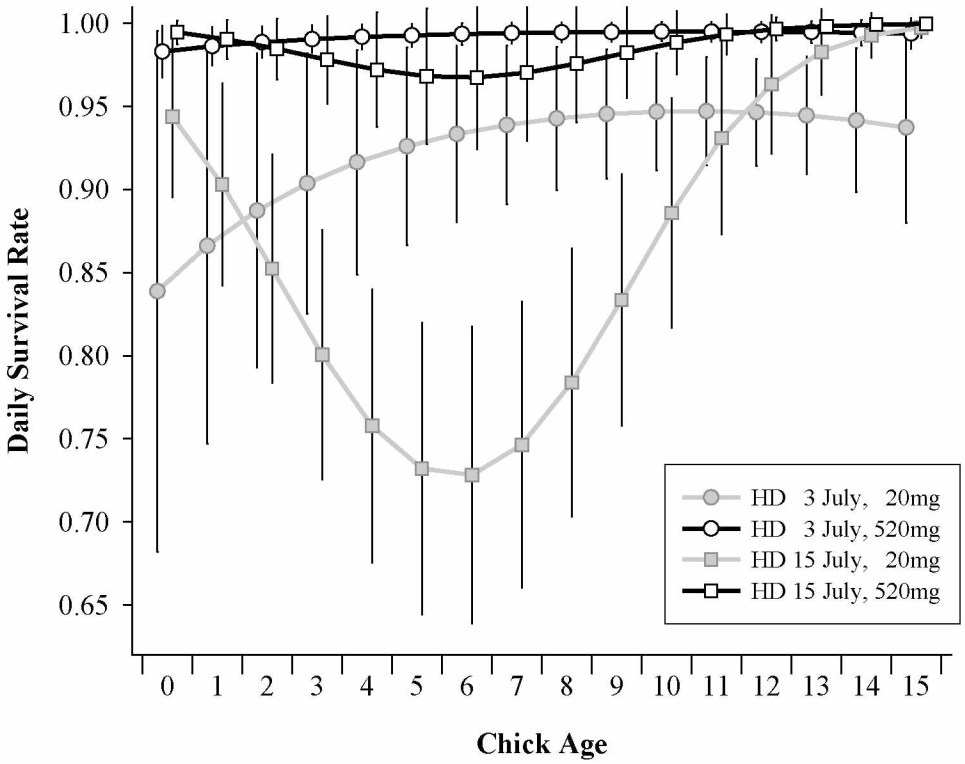

Figure 2.7. Estimated daily survival rates (± 1 SE) of Dunlin chicks as a function of age (A), hatch date (HD), and insect biomass (dry weight; I) from the top model (I + HD + A + A^2 + HD*A + HD*A^2). Estimates are presented for average hatch dates for initial nests (3 July) and early and late replacement nests combined (15 July), and for low and high insect biomass. Symbol locations represent the same chick age for each combination of hatch date and insect biomass but lines are offset so SEs are visible.

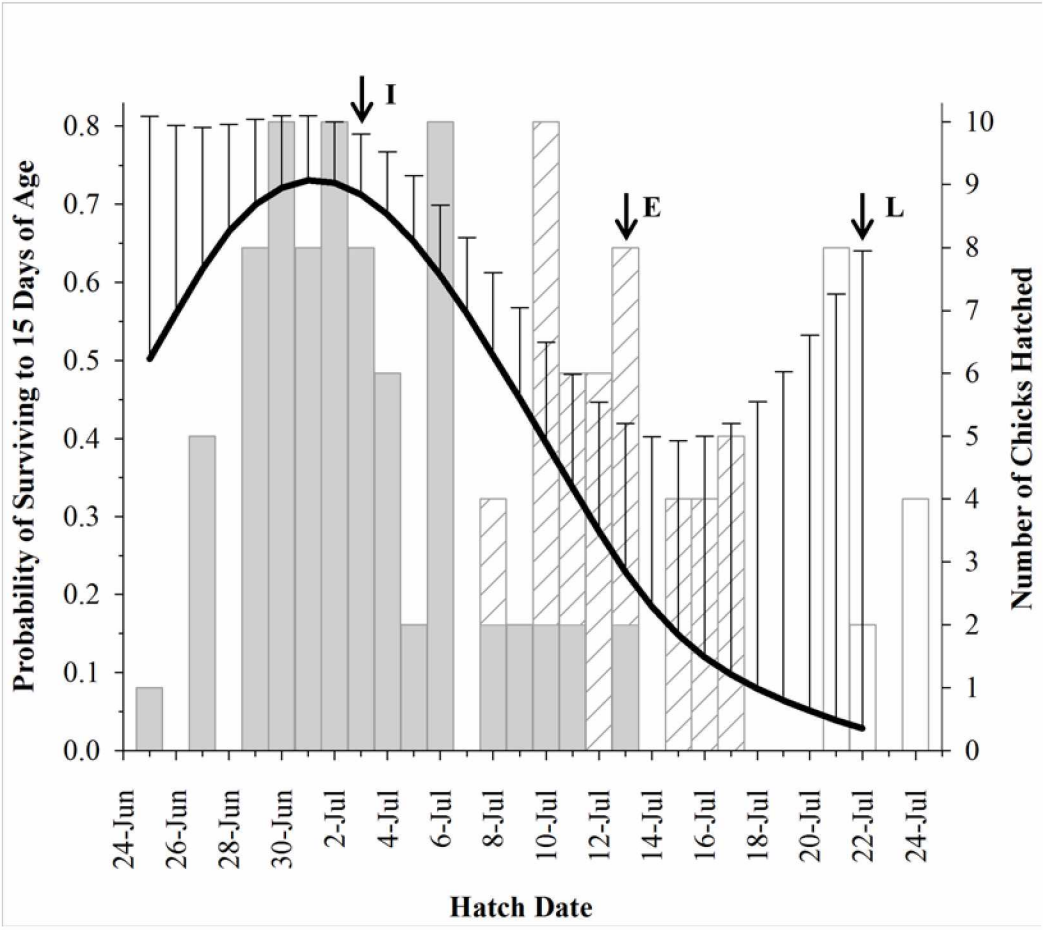

Figure 2.8. Estimated probability of a Dunlin chick surviving to 15 days of age as a function of hatch date (solid line, only positive SE displayed). Bars show the number of chicks hatched per day, and arrows show the average hatch date for initial (I; gray), early replacement (E; diagonal), and late replacement (L; white) nests in 2008 and 2009 combined. The latest hatch date that data are available to estimate the probability of surviving to 15 days of age is 22 July.

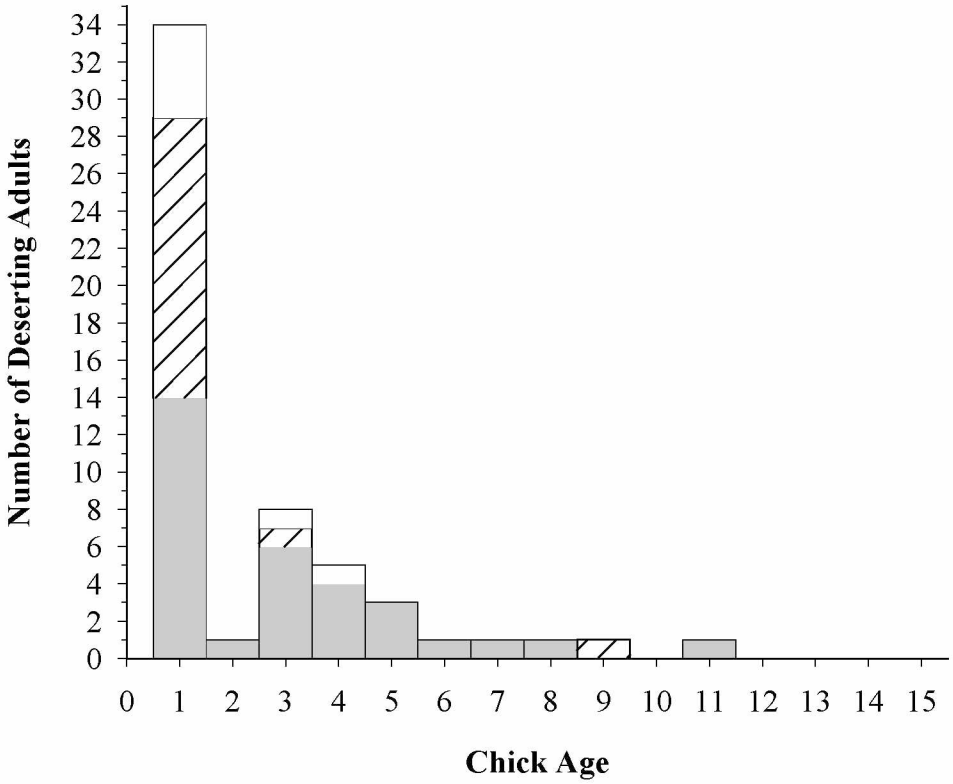

Figure 2.9. Number of deserting adults in relation to chick age for Dunlin in 2008 and 2009. Data limited to the first marked adult to desert their brood prior to brood failure or survival of at least one chick to 15 days of age (n = 56). For all but one brood (where both parents deserted), a second parent continued to attend the brood until brood failure or survival of at least one chick to 15 days of age. Stacked bars show adults from initial (gray), early replacement (diagonal), and late replacement (white) nests.

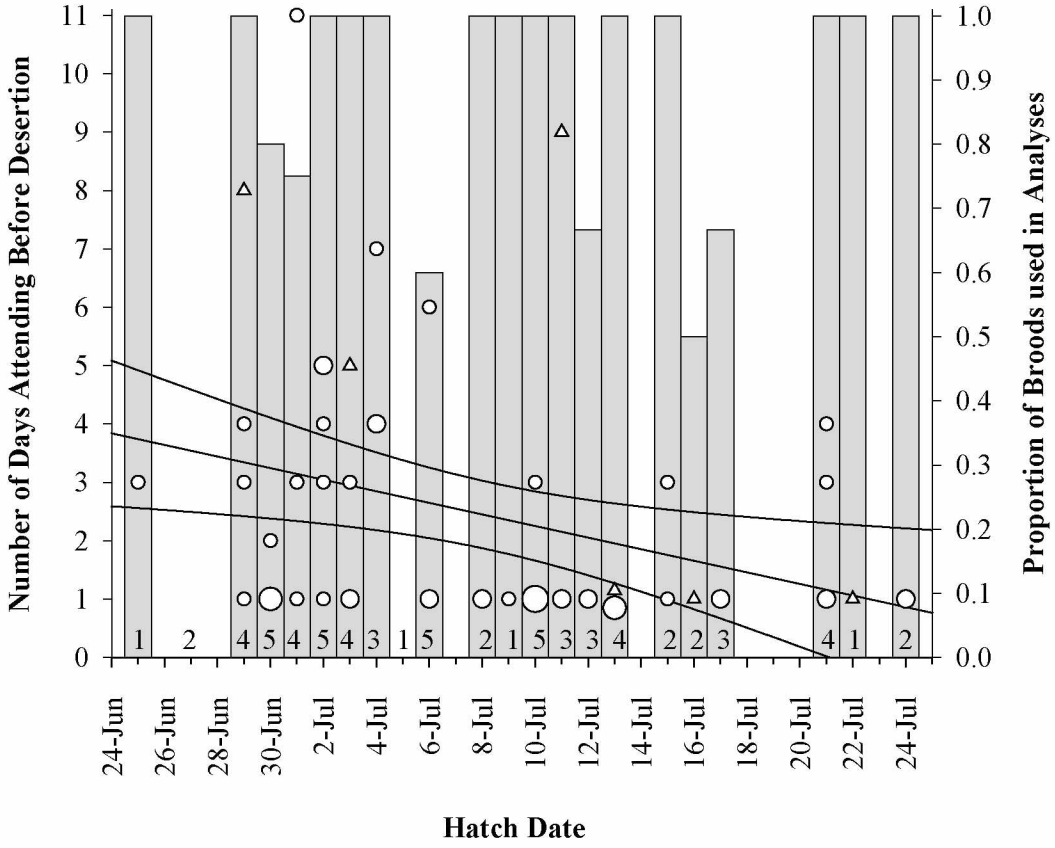

Figure 2.10. Attendance time of Dunlin that deserted their brood in relation to hatch date in 2008 and 2009. All but one of 66 broods were still being attended by one parent at time of death or survival to 15 days of age. In the one exception, both adults deserted while the brood was still active, but only data from the first adult to desert this brood is used in the analyses. Ten broods were excluded because both parents were present when the brood died (n = 6) or one parent was not marked (n = 4). The number of days attending prior to desertion = -0.10*hatch date + 3.83. r^2 = 0.11 and 95% CIs are shown. The proportion of broods (sample size above x-axis) used in the analysis are indicated by gray bars. Symbol type: females = circles, males = triangles. Symbol size: smallest = 1 adult, largest = 4 adults. Data on the 13 July are slightly offset so symbols are visible.

Figure 2.11. Illustration of the difference in growth rates of Dunlin chicks in relation to hatch date and nest category in 2009. Hatch dates are 9 July, 12 July, and 13 July, for chicks 1, 2, and 3 respectively. Chick 1 was from an initial nest, while chicks 2 and 3 were from early replacement nests. Although these chicks had similar hatch dates, and thus experienced similar environmental conditions and food availability, chicks 2 and 3 appear to have grown more slowly than chick 1. Although anecdotal, these observations suggest there may be differences in egg quality between initial and replacement nests.

Table 2.1. Number of potential chick predators and lemmings observed in 2008 and 2009. Counts were conducted in: 1) the un-manipulated area, and 2) the greater Barrow area, encompassing Point Barrow and south to approximately 71°20"N (see Fig. 2.1). Weasel and lemming data are from the chick-rearing period (25 June – 6 August).

	2008	2009	Survey Area	Reference
Snowy Owl Nests	35	0	Greater Barrow	D. Holt unpubl. data
Pomarine Jaeger Nests	6	0	Un-manipulated Plots	R. B. Lanctot unpubl. data
Active Fox Dens	11	0	Greater Barrow	Gilsdorf and Rossi 2008, Savory et al. 2009
Adult Fox Killed	45	12	Greater Barrow	Gilsdorf and Rossi 2008, Savory et al. 2009
Weasels (total obs./season)	16	0	Greater Barrow	R. B. Lanctot unpubl. data
Lemmings (avg. # obs./person/day)	12.74	0.02	Greater Barrow	R. B. Lanctot unpubl. data

Table 2.2. Model selection for daily survival rate of Dunlin chicks in relation to hatch date (as a linear, HD, or quadratic function, $HD+HD^2$), chick age (as a linear, A, or quadratic function, $A+A^2$), insect biomass (I), temperature (T), and year (Y) in 2008 and 2009. Only models with $\Delta QAIC_c$ values < 4.0 are presented. $QAIC_c$ = Akaike's information criterion corrected for sample size and overdispersion ($\hat{c}$ = 3.14); $\Delta QAIC_c$ = difference in $QAIC_c$ values between the current and top model; K = number of parameters; QDeviance = quasi-likelihood deviance. See text for description of the model set.

Model	Δ $QAIC_c$	$QAIC_c$ Weights	K	QDeviance
$I + HD + A + A^2 + HD*A + HD*A^2$	0.00	0.09	7	119.53
$I + HD$	0.74	0.06	3	128.33
$HD + A + A^2 + HD*A + HD*A^2$	0.86	0.06	6	122.41
$I + A$	1.02	0.05	3	128.61
HD	1.12	0.05	2	130.72
$I + A + A^2$	1.36	0.05	4	126.95
$I + HD + I*HD$	1.75	0.04	4	127.33
$I + A + A^2 + I*A + I*A^2$	2.08	0.03	6	123.63
I	2.10	0.03	2	131.70
$I + HD + A$	2.28	0.03	4	127.86
$Y + HD + A + A^2 + HD*A + HD*A^2$	2.53	0.03	7	122.06
$I + HD + A + A^2$	2.66	0.02	5	126.23
$I + HD + HD^2$	2.68	0.02	4	128.26
$I + Y + HD$	2.71	0.02	4	128.29
$Y + HD$	2.85	0.02	3	130.45
$HD + A$	2.97	0.02	3	130.56
$I + A + I*A$	3.01	0.02	4	128.59
$I + Y + A$	3.03	0.02	4	128.61
$HD + HD^2$	3.03	0.02	3	130.63
$HD + I + A + A^2 + I*A + I*A^2$	3.27	0.02	7	122.80
$I + Y + A + A^2$	3.37	0.02	5	126.94
$HD + A + A^2$	3.50	0.02	4	129.08
$I + Y + HD + I*HD$	3.68	0.01	5	127.24
$I + HD + A + HD*A$	3.75	0.01	5	127.31
$I + Y + HD + Y*HD$	3.86	0.01	5	127.42

General Conclusions

Accurate demographic parameter estimates and an understanding of the relationship of parameters to factors potentially impacting a population can provide insight into the cause of population trends and help identify what management actions would most benefit a population. This can be especially important for declining populations. While previous studies on shorebirds have indicated the large negative role of low adult survivorship on population growth rates (Hitchcock and Gratto-Trevor 1997, Sandercock 2003, Ottvall and Härdling 2005, Koivula et al. 2008), juvenile survival and productivity will also be important to population growth for species with moderate adult survival.

Dunlin (*Calidris alpina arcticola*) that breed in arctic Alaska and overwinter in Asia are thought to be declining (Fernández et al. 2008, Amano et al. 2010). These declines may be due to loss of intertidal habitat on their non-breeding grounds in Asia, habitat that is necessary for overwinter survival (Fernández et al. 2008, Amano et al. 2010). While surveys have been conducted on Dunlin populations in arctic Alaska (Brown et al. 2007, Bart et al. 2012) and Asia (Amano et al. 2010), it is difficult to distinguish changes in population abundance from changes in distribution. Estimating survival and other demographic rates and combining those estimates in demographic models provides a more robust method for evaluating changes in populations.

I estimated survival probabilities for *arcticola* Dunlin adults and chicks at an arctic breeding site near Barrow, Alaska, USA. In chapter one I estimated re-sighting and apparent survival probabilities of adult Dunlin using Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965) and data collected between 2003 and 2010. I evaluated whether re-sighting and/or survival probabilities were affected by individual-level qualities (individual nest success, individual nest initiation date), population-level variables (the timing of spring snow melt, average nest success, fox control), habitat variables (completion of the Saemangeum Dike), or sex. I found that the sex of an individual most affected the probability of re-sighting, with males having a higher

probability (0.89, 95% CI: 0.82 – 0.93) than females (0.73, 95% CI: 0.61 – 0.82). This difference in re-sighting rates between the sexes has been observed in other shorebirds (Holmes 1971, Gratto et al. 1985, Paton 1994), and is likely a result of males being more visible than females (Holmes 1966, Lanctot et al. 2000, Schekkerman et al. 2004) and males being less likely to emigrate from the study area than females (Soikkeli 1967, Gratto et al. 1985, Jackson 1994, Clarke et al. 1997, Thorup 1999).

Survival rates were higher for males than females, and were higher the earlier a nest was initiated. Individuals initiating nests just 10 days after the average initiation date for the population had an 11 – 31% lower survival probability (depending on sex and year). Birds nesting earlier may have higher survival rates because they are returning breeders and are therefore more experienced (Heldt 1966, Soikkeli 1967, Gratto et al. 1983, Thompson et al. 1986, Lanctot et al. 2000, Johnson and Walters 2008). These individuals could have an advantage over less experienced individuals if they can pair more quickly (especially if they retain the same mate as the prior year), thereby avoiding the costs associated with mate attraction displays (Lanctot et al. 2000); if they benefit from having knowledge of good quality nesting and foraging habitat (Oring and Lank 1984); or if they arrive in better condition. Several studies have indicated that the heaviest individuals (i.e., those in better condition) observed during migration were more likely to be re-sighted in subsequent years (e.g., Drent et al. 2003, Baker et al. 2004). Nesting earlier also allows more time to prepare for southward migration.

Males had higher survival rates (0.89, 95% CI: 0.82 – 0.93) than females (0.73, 95% CI: 0.61 – 0.82) in all years of the study. This has also been documented in congeners (Western Sandpipers, Johnson et al. 2010; and Semipalmated Sandpipers, Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000), and may indicate that females suffer higher mortality due to higher costs of reproduction than males. A clutch of Dunlin eggs is approximately 76% of the weight of a female (Gates 2011), representing a large energy investment. Females also endure costs associated with incubation duties, although they typically do not attend broods (see chapter two). Males, on the other hand, expend energy attracting a mate (although this is can be minimal when

pairing with a prior mate, Lanctot et al. 2000), defending their territory (Holmes 1966), incubating eggs, as well as rearing a brood. In the event of nest failure however, males are relieved of their incubation and brood-rearing duties, removing much of their reproductive costs, whereas females still experience high reproductive costs through energy expended laying eggs. Following nest failure, females may lay a second clutch of eggs, adding additional reproductive costs. Our estimates of lower female survival may also be an artifact of higher permanent emigration in females than males. However, because survival and emigration are confounded in Cormack-Jolly-Seber modeling, I could not evaluate this with my data. But, female dispersal of Dunlin and congeners has been documented (Jackson 1994, Thorup 1999, Sandercock et al. 2000, Jehl Jr. 2006). Lower female survival may also be a result of higher mortality rates of females during migration or on the wintering grounds, for example if males and females segregate and experience different levels of habitat alteration. Sex segregation has been documented in Western (Nebel et al. 2002) and Least Sandpipers (Nebel 2006), though is unknown for the *arcticola* Dunlin subspecies.

Survival probabilities also varied annually, with particularly high variation in the first three years. However, variables I investigated that represented patterns in survival among years were not supported. Although I predicted that major habitat loss and fox control in Asia would negatively affect survival of adult Dunlin these variables were not supported. Individual-level qualities (e.g., individual nest initiation date) were more supported than these population-level qualities (and others) suggesting that individual variation characterizes differences in survival probabilities more so than yearly variation in population-level characteristics.

In chapter two, I estimated the survival of Dunlin chicks in 2008 and 2009 from initial (first) and replacement nests. Replacement nests were artificially derived by experimentally removing first nests from Dunlin pairs and locating the subsequent replacement nest. Because chicks were radio-tagged, I used known-fate modeling and generated daily survival rates (DSR) based on 75 *a priori* models incorporating factors previously found to affect chick survival. I predicted that survival rates would be

positively correlated with age (Soikkeli 1967, Schekkerman et al. 1998, Pearce-Higgins and Yalden 2002, Ruthrauff and McCaffery 2005), insect biomass (Schekkerman et al. 2003, Tulp 2007), and temperature (Beale et al. 2006, Soloviev et al. 2006, Meltofte et al. 2007, Tulp 2007), and would be negatively related to hatch date (Soikkeli 1967, Ruthrauff and McCaffery 2005, Tulp 2007, Hartman and Oring 2009). The latter prediction would result in chicks from initial nests having higher survival than chicks from replacement nests.

I found that insect biomass, chick age, and hatch date were the variables that most affected chick DSR. Insect biomass positively affected DSR for all chick ages and hatch dates. However, there was a complicated relationship between hatch date, chick age, and insect biomass. In general, at high insect biomasses, early hatching chicks had high and stable DSR in relation to age, while those hatching later had a slight decrease in DSR around one week of age. At low insect biomasses, early hatching chicks had DSR that increased until 12 days of age and then slightly decreased, while chicks hatching later had a dramatic decrease in DSR at one week of age. Anecdotally, I found that chicks from replacement nests appeared to grow slower than chicks from initial nests, even if they hatched near the same date. Slower growth of chicks from replacement nests could be one reason for the different relationship of DSR with age and insect biomass for later hatching chicks.

The probability that a chick survived to 15 days of age (the age at which I first saw chicks flying) was highest for chicks from initial nests. Chicks from initial nests survived at higher rates (0.71 ± 0.07) than chicks from either early (0.23 ± 0.19) or late (0.03 ± 0.61) replacement nests. Even though prior studies have found that survival decreases across a season, studies that compared survival of young from initial and replacement nests have found mixed results (Verboven and Visser 1998, Hipfner 2001, Arnold et al. 2004, Yasué and Dearden 2008, Bettega et al. 2011, Jamieson 2011). I conclude that survival of chicks from replacement nests is much lower than survival of chicks from first nests, and these results suggest that replacement nests make a much smaller contribution to productivity than first nests. The survival rates in my study area

are likely biased high due to the fact that arctic fox (a top predator) were actively removed during the two years of my study. It is unknown how much fox predation impacts chick survival, but based on the large role they play in shorebird nest predation (Summers et al. 1998, Liebezeit and Zack 2008, McKinnon and Bêty 2009), it is not unreasonable to suggest they could also play a large role in chick predation. A similar study conducted in an area without fox control could help determine whether predator control enhances chick survival.

Early breeding adults and early hatching chicks at my study site survived better than those breeding or hatching later. I speculate that individuals breeding or hatching later may not subsequently be able to adequately prepare for southbound migration, although Dunlin are known to stage on the northern coast of Alaska until early to late August, and again farther south at the Yukon-Kuskokwim Delta until early October (Taylor et al. 2011). While this suggests they have ample time to prepare for migration, later-arriving individuals could suffer from prey depletion at staging areas, leading to poorer body condition and reduced over-winter survival (reviewed by Newton 2006). Thus, negative consequences may be experienced later in the year for those that finish breeding or fledging later.

The adult survival probabilities generated from my study are quite alarming. Though similar to other small sandpiper survival rates (Colwell 2010), previously conducted demographic analyses indicated that survival rates at these levels were not high enough to sustain population levels (Hitchcock and Gratto-Trevor 1997, Ottvall and Härdling 2005, Koivula et al. 2008). These results suggest that, similar to congeners, Dunlin survival rates are too low and are likely a major cause of apparent population declines. High chick (and subsequently, juvenile) survival may compensate for low adult survival rates in some years. In years of high nest survival, adults presumably lay fewer replacement nests, and likely fledge more young. In years of low nest survival however, most nests are likely replacement nests, resulting in low production of young. Recruitment into the population therefore would be low and would likely not compensate for low adult survival.

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